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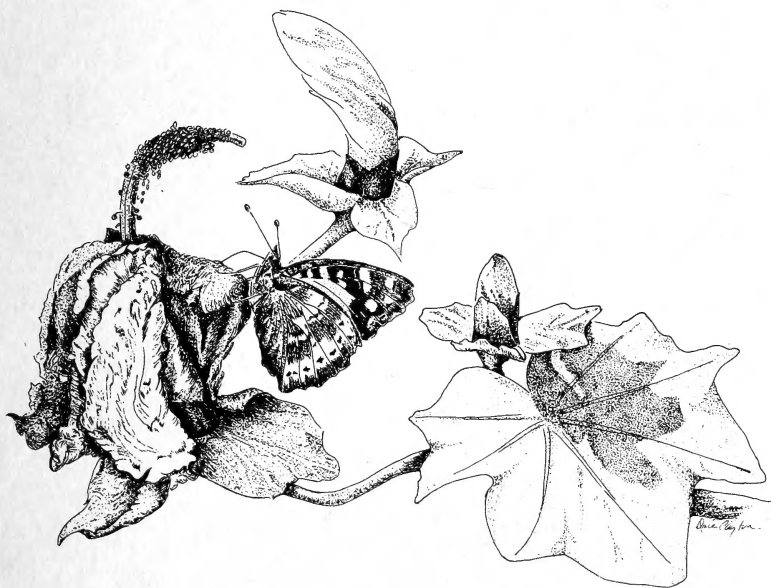
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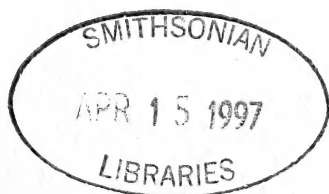
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Cover illustration: "old friends"—the endemic Hawaiian nymphalid, *Vanessa tameamea*, feeding at a wilted and senescent flower of the endemic plant, *Kokia kauaiensis*. Original pen and ink drawing by Dale Clayton, Dept. Biol. Sciences, Southwestern Adventist College, Keene, Texas 76059, USA.

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PRESIDENTIAL ADDRESS 1996: ON THE BEAUTIES, USES, VARIATION, AND HANDLING OF GENITALIA

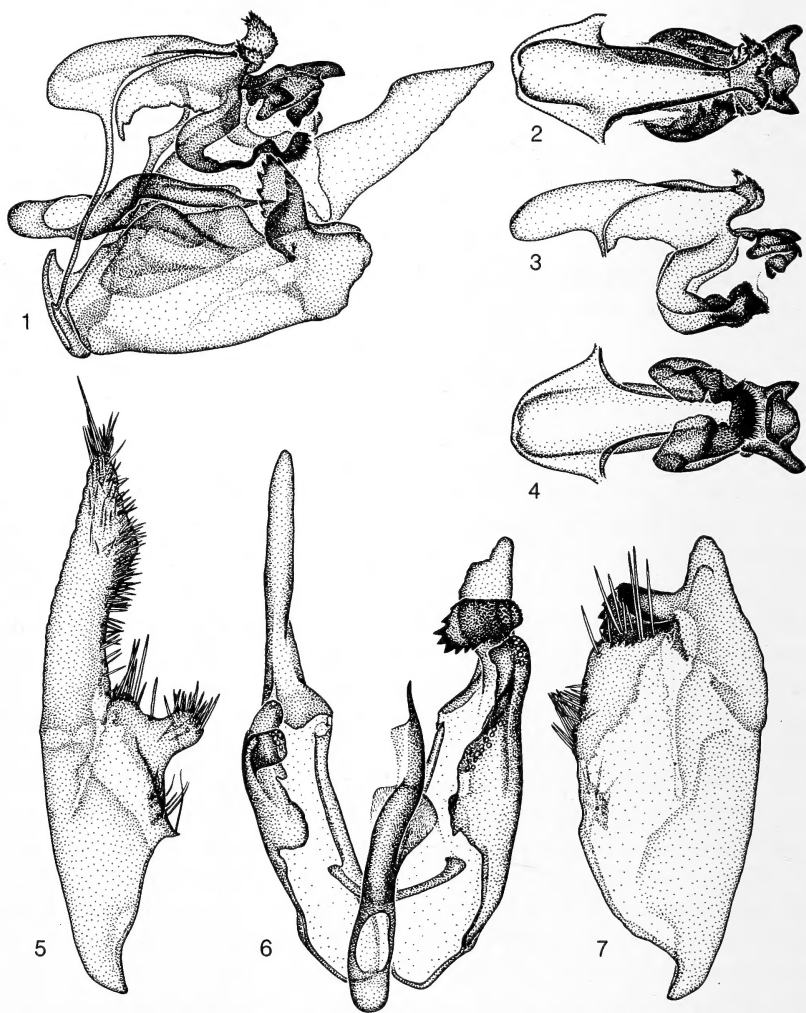
JOHN M. BURNS

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Thanks to *Erynnis*, I got hooked on genitalia at an impressionable age (Burns 1964). Although some measure of genitalic asymmetry is not rare in hesperiids, *Erynnis* is the only skipper genus with thoroughly asymmetric genitalia that is widespread in North America north of Mexico. I welcomed rampant genitalic asymmetry because it added spice to comparative morphology and greatly increased the number of characters in structures that are taxonomically useful anyway (Figs. 1-7).

Back when few American species of *Erynnis* were known and the taxonomic use of genitalia was not yet in vogue, Scudder and Burgess (1870) seized on the asymmetric genitalia—and nothing but those genitalia—in distinguishing and describing not only the known species of *Erynnis* but also a number of new ones (much to the indignant annoyance of some contemporaries who refused to accept them). The only valid criticism is that Scudder and Burgess did not compare enough genitalia to appreciate individual variation fully and so described four species more than once.

The value of genitalia for distinguishing species can hardly be overstated. In trying to show how to separate two large, similar looking but none too closely related, eastern North American species of *Erynnis* superficially, Klots (1951:pl. 29, figs. 7, 9) indicated, with photographs of males, the presence of two subapical white spots on the ventral hindwing in *E. juvenalis* (Fabricius) and their absence in *E. horatius* (Scudder & Burgess). I have examined the genitalia of his models (which Klots clearly labelled as such) and found both to be *E. juvenalis*. The tegumen, uncus, and dissimilar left and right valvae of *E. juvenalis* (Scudder & Burgess 1870:figs. 9, 10) depart widely from those of *E. horatius* (Scudder & Burgess 1870:figs. 13, 14). Although the uncus and left and right valvae of *E. horatius* closely resemble those of its para-



FIGS. 1-7. Strikingly asymmetric male genitalia of the pyrgine skipper *Erynnis scuderi* (Skinner) which ranges from southeastern Arizona, USA, to Guatemala; specimen from the El Tapon area, route CA 1, 5600 ft [1705 m], GUATEMALA, 8 August 1971, R. W. Holland (J. M. Burns genitalia no. 1360) (USNM). **1**, Complete genitalia in left posterodorsolateral view. **2-4**, Tegumen, uncus, and gnathos in dorsal, lateral, and ventral views, with posterior end to right (structures turned ninety degrees between successive views). **5**, Right valva in right lateral view (spines included). **6**, Both valvae plus aedeagus in dorsal view (spines omitted). **7**, Left valva in left lateral view (spines included). In last three views, posterior end at top; and each valva shown at two angles, ninety degrees apart. Drawings by Robin S. Lefberg.

TABLE 1. Forewing length (mm) in genitically identical species of *Erynnis* taken by J. M. Burns in association with their larval foodplants either in (*E. baptisiae*) or near (*E. lucilius*) Middletown, Connecticut, USA, between 1962 and 1965.

Species	Phenotype	Sex	N	Range	Mean	SE	SD	CV
<i>E. lucilius</i>	1	♂	43	12.4–15.2	13.89	0.12	0.81	5.83
	1	♀	13	13.6–15.4	14.50	0.18	0.66	4.55
	2	♂	17	13.8–15.9	15.04	0.14	0.58	3.86
	2	♀	8	14.2–17.0	15.69	0.30	0.86	5.48
<i>E. baptisiae</i>	1	♂	32	13.4–16.2	15.13	0.13	0.72	4.76
	1	♀	31	14.1–17.5	15.57	0.14	0.77	4.95
	2	♂	45	14.7–17.8	16.26	0.09	0.63	3.87
	2	♀	21	16.1–18.5	17.25	0.15	0.70	4.06

patric, western American sister species, *E. tristis* (Boisduval) (Scudder & Burgess 1870:fig. 15), the distal end of the tegumen, which is divided, forms a long, fat finger on the right side in *E. horatius* but a large, round plate on the left in *E. tristis*.

Of course, the genitalia do not have to vary between species. Even in *Erynnis*, with its rich asymmetry, I have tried and failed repeatedly over the years to discover at least one genitalic difference between *E. baptisiae* (Forbes), a more southern, eastern North American differentiate that feeds as a larva primarily on *Baptisia*, but also on *Lupinus*, and now, secondarily, on an introduced *Coronilla* (all Fabaceae), and *E. lucilius* (Scudder & Burgess), a more northern sister differentiate that departs evolutionarily from its congeners by eating *Aquilegia* (Ranunculaceae). However, where these two skippers coexist in central Connecticut, I can statistically demonstrate a difference in the size of adults sampled in direct association with their larval foodplants, *Aquilegia canadensis* L. and *Baptisia tinctoria* (L.) R. Br. I know from my prior detailed analysis of variation in size that, within a species of *Erynnis*, females average larger than the males with which they fly and that summer generation individuals (phenotype 2) in either sex average larger than spring generation individuals (phenotype 1) of the same sex (Burns 1964). After appropriate subsampling, *E. baptisiae* consistently averages at least one millimeter longer than *E. lucilius* in forewing length (Table 1).

Across the genus *Erynnis* as a whole, I encountered such enormous genitalic variation that for years I implicitly accepted, or tolerated, wide genitalic latitude within skipper genera generally. This was a mistake. Genitalia are often phylogenetically constrained—so much that they offer characters of special value in grouping at the generic level (and above), along with those that serve in telling species apart. History did not help my perception, either, because pioneers (like Scudder & Burgess 1870, Scudder 1889, Godman & Salvin 1879–1901) in the use of male genitalia in distinguishing skipper species, failed to see the

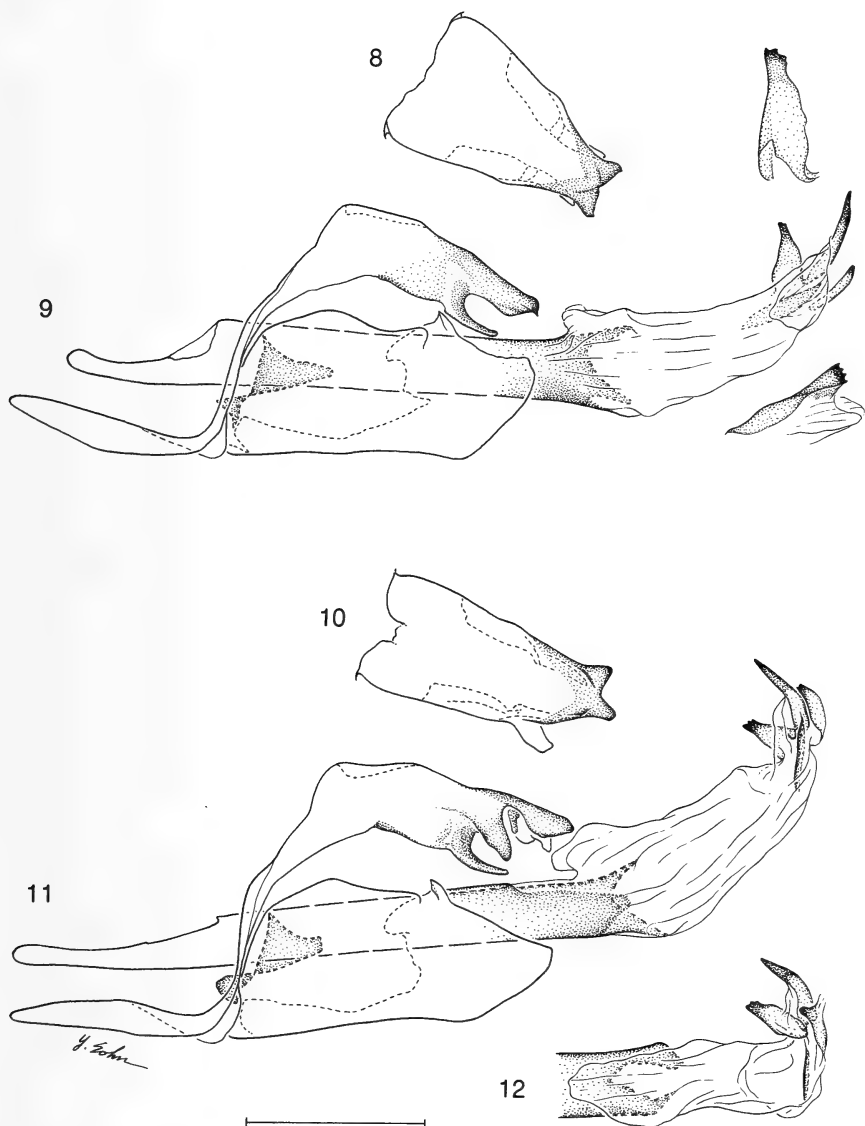
higher level information at hand and frequently put species with similar genitalia in different genera and species with quite different genitalia in the same genus. Only in the last decade have I fully realized that many of our much-studied and long-stable nearctic skipper genera (as well as many poorly studied neotropical ones) are polyphyletic and that genitalia (in both sexes) provide crucial tools for sorting them out (see Burns 1994, 1996, plus earlier papers cited therein).

Though I lean heavily on genitalia in redefining genera, I always seek supporting information. After pulling three long-tailed species out of *Polythrix* and uniting them, on genitalic grounds, with tailless species in the distant, supposedly monotypic genus *Cephise*, I found that all species in much-expanded *Cephise* share a unique palpal feature and that both tailed and tailless species eat the same larval foodplants (Burns 1996).

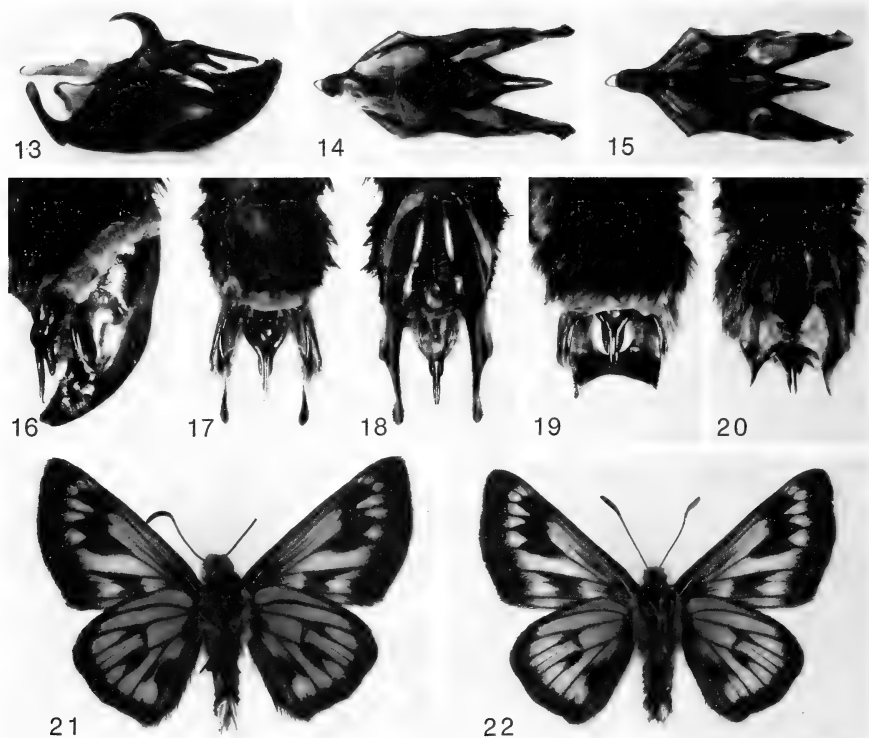
Despite its loss, "*Polythrix*," a neotropical genus of similar appearing tailed species, is still so genitally heterogeneous and polyphyletic that what remains may go in six different genera. True *Polythrix* are the type species, *metallescens* (Mabille), as well as *kanshul* Shuey and *eudoxus* (Stoll) (Burns 1996). The largest genitally compact unit that does not include the type species is the *asine* group of six: *asine* (Hewitson), *gyges* Evans, *hirtius* (Butler), *mexicanus* Freeman, *roma* Evans, and an undescribed species. Another genitally compact unit is the *auginus* group of three: *auginus* (Hewitson), *caunus* (Herrich-Schäffer), and an undescribed species. Three species are genitalic oddballs: *ceculus* (Herrich-Schäffer), *minvanes* (Williams), and *octomaculata* (Sepp).

Genitalia express plenty of individual variation, which must be studied, compared, and understood in order to interpret them correctly. As noted above, Scudder and Burgess (1870) were initially overimpressed by minor genitalic variants and described too many species of *Erynnis*, no doubt because they looked at few individuals. In the course of examining some 12,000 genitalia during microevolutionary studies of *Erynnis*, I uncovered occasional major variants, the most stunning of which are males of *E. funeralis* and *E. propertius* (both species described as new by Scudder and Burgess in 1870) whose genitalia are secondarily symmetric: the left valva is a mirror image of the right one instead of its usual, highly distinctive self (Burns 1964, 1970:figs. 1–4).

Among numerous genitalic dissections connected with an ongoing generic redefinition and revision, I have found—in just one of a few males of an undescribed neotropical species—the reverse situation where genitalia that are normally symmetric (except for the distal aedeagus and its cornuti) are, all at once, conspicuously asymmetric in both the tegumen and the uncus (Figs. 8–12). Again, one of six males of an undescribed species in the *asine* group of "*Polythrix*" from El Salvador and Costa Rica has abnormal spikes directed downward from the ven-



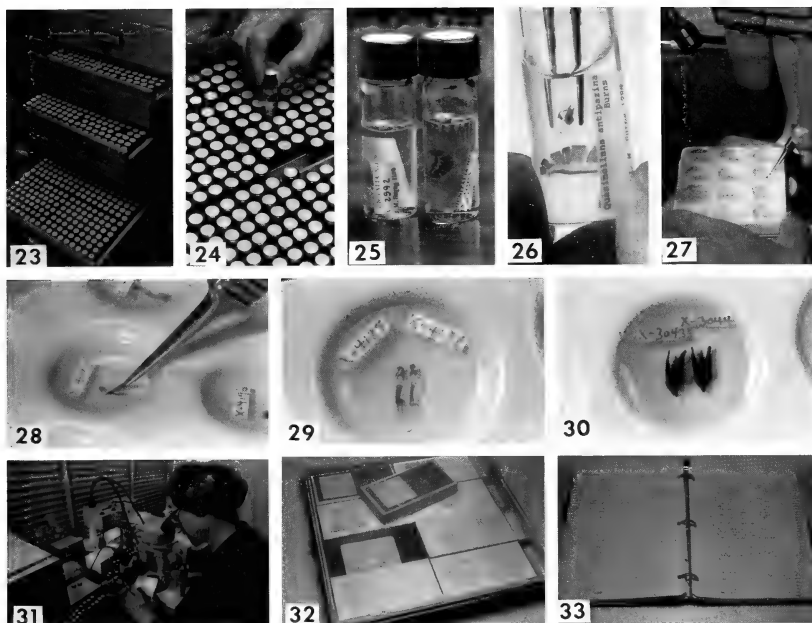
FIGS. 8–12. Bizarre variation in male genitalia of an undescribed hesperiine skipper that ranges from Mexico to Colombia or Ecuador (Burns, unpubl. data). **8, 9**, Normal genitalia from Santa Rosa, Veracruz, MEXICO, May 1906 (J. M. Burns genitalia no. X-3037) (USNM). **10–12**, Abnormal genitalia—with a major process (unknown in this and other, related, genera) arising (only on the left side) from the tegumen/uncus, above the base of the gnathos; a bend to the right at the distal end of the uncus; and a uniquely low dorsodistal edge on the valva—from Chiriquí, PANAMA (J. M. Burns genitalia no. X-3862) (Museum für Naturkunde der Humboldt-Universität zu Berlin, Zoologisches Museum). **8, 10**, Tegumen, uncus, and gnathos in dorsal view. **9, 11**, Complete genitalia (minus right valva), with vesica everted to show quadruple cornuti, in left lateral view (plus, in **9**, enlargements of two cornuti at different angles). **12**, Distal end of aedeagus, with vesica everted to show quadruple cornuti, in dorsal view. Drawings by Young Sohn.



FIGS. 13–22. Devastating variation in male genitalia of the pyrrhopygine skipper *Metardaris cosinga* (Hewitson) from the department of Cuzco, 2850 m, PERU. **13–15**, Normal genitalia (boiled in 10% KOH, freed from other sclerotized parts, cleaned of scales, muscles, etc., and stored in glycerol) in left lateral, dorsal, and ventral views; from 5 km N Paucartambo, 13°15' S, 71°37' W, 28 August 1989, R. K. Robbins (J. M. Burns genitalia no. X-3044) (USNM). **16–18**, Normal genitalia (dissected dry in situ) in right lateral, dorsal, and ventral views; same field data as preceding male (USNM). **19, 20**, Abnormal genitalia (dissected dry in situ)—with massive cross-fusion between the bottoms of the valvae, or claspers, making the genitalia totally useless—in dorsal and ventral views; from near Calca, 13°19' S, 72°00' W, 27 August 1989, D. J. Harvey (USNM). **21, 22**, The whole skippers, with their dry-dissected genitalia exposed, in ventral view: normal on left, abnormal on right. Photographs by Carl C. Hansen.

tral edges of its valvae near their distal ends, one on the left and two on the right. Taxonomists who do not set variation in a proper context might describe each of these two aberrant males as new for the wrong reasons.

But could anyone misinterpret the male of *Metardaris* that leaped out at me from others in a batch of newly spread skippers because the distal end of its abdomen was strangely chafed? A victim of grossly deviant development that broadly joined both valvae ventrodistally (Figs. 13–22)—to create a sort of built-in, indestructible chastity belt—it must have



FIGS. 23–33. Handling, study, and storage of liberated skipper genitalia. **23**, Cabinet drawers with rows of one-dram, screw-cap vials holding genitalia (and usually also abdominal skins) in glycerol. **24**, Removing a vial from its numerical sequence in a drawer (individual dissection numbers on round adhesive labels on the tops of vials). **25**, Two one-dram vials showing dissections and permanent labels with individual dissection numbers inside. **26**, Removing dissected genitalia from a vial with forceps (here, an accessory sex- and-determination label accompanies the mandatory dissection label). **27**, Genitalia with temporary tags in glycerol in a 12-depression, porcelain spotplate for critical microscopic study and comparison. **28**, Manipulating female genitalia in a spotplate depression with jeweler's forceps. **29**, Directly comparing two female genitalia in a single spotplate depression. **30**, Directly comparing two male genitalia in a single spotplate depression (the genitalia on the right [X-3044] appear, larger than life, in Figs. 13–15). **31**, John Burns closely comparing genitalia at his work desk with variable lights and a stereomicroscope. **32**, Temporary storage of spotplates of genitalia during long, large projects: plates in a USNM insect drawer, with half-column pinning units upside down to serve both as dust covers and as surfaces for sticky notes on the dissection numbers, sexes, identities, sources, and peculiarities of the covered genitalia. **33**, Facing pages of the requisite dissection notebook showing, for each genitalic preparation, a one-line entry beginning and ending with the dissection number, and including sex, determination, parts dissected, date of dissection, time boiled in KOH, and the date, locality, and collector of the specimen, as well as the collection in which the specimen resides. *Photographs by Chip Clark.*

spent most of its short adult life attempting basic copulatory motions (such as clasping with its claspers) which fizzled, ruffling it and its posterior scales. No ardent conservationist can ever censure the untimely human capture of this specimen (Figs. 19, 20, 22) since it already had been naturally selected against.

From the beginning I have handled genitalia in a novel but expedient

manner (Figs. 23–33). I keep them free in vials because slide mounts may distort them and will always severely limit the angles of view and preclude side-by-side comparisons. I use large, one-dram screw-cap vials (with an inverted plastic cone in the cap) which readily hold the abdominal skin unfolded, as well as the dissected genitalia, a label with the dissection number, and, if desired, another with sex and determination—all in enough glycerol to last until the next glaciation (Figs. 25, 26). Genitalia and skins can be examined superficially within vials and can easily be removed from them with forceps for detailed study. Microvials (especially older ones with cork stoppers) dry out over time, leak on occasion, require folding of skins and large genitalia, need to be pinned, may suffer stopper breakage, and are generally messier and harder to handle. For all-important repeated study and direct comparison at each and every possible angle, I keep genitalia in glycerol in spot-plate depressions with temporary tags, often for years at a stretch (Figs. 27–32). There is no better way.

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DIVERSITY AND EVOLUTION OF TONGUE LENGTH IN HAWKMOTHS (SPHINGIDAE)

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ABSTRACT. Hawkmoths are best known as long-tongued nectar foragers, but as many as one-fifth of hawkmoth species have drastically shortened tongues and do not seek flower nectar. Clues to tongue-length diversity and evolution have not previously been sought in any hawkmoth stage but the adult. Using comparative methodology, and investigating some 150 species of New and Old World hawkmoths, I uncover correlations between tongue length and latitude of distribution, and between tongue length and growth form of larval foodplants. Through north latitudes ranging from 0 to 40 or 50°, mean tongue length declines worldwide from more than 40 mm to 15 mm or less. Through larval foodplant growth-form indexes ranging from 2 (herbs) to 6 (trees), mean tongue-length similarly declines from more than 40 to less than 15 mm. I speculate for extratropical regions that tongues have lengthened in hawkmoths that must imbibe large amounts of nectar as flight fuel to find inconspicuous, nonpersistent larval foodplants such as herbs, whereas tongues have shortened in hawkmoths that have the easier task of finding conspicuous, persistent larval foodplants such as trees. Residual tongue-length variation could reflect miscellaneous factors operating at smaller than continental geographic scales.

Additional key words: growth form, pollination, geographic variation, phylogenetic analysis.

The long proboscis or tongue is a hallmark of Sphingidae. The tongue of the neotropical *Amphimoeca walkeri* (Bdv.), whose length can reach 280 mm (Amsel 1938), is thought to be the longest haustellum in all Insecta. Also contributing to sphingid tongue lore is the story of the Madagascan hawkmoth *Xanthopan morgani praedicta* R. & J. (Kritsky 1991). Charles Darwin observed in 1862 that the nectar of the Madagascan star orchid, *Angraecum sesquipedale* Thouars (Orchidaceae), is hidden some 290 mm deep in the blossom. A hawkmoth pollinator with so long a tongue was then unknown, but Darwin predicted that one would be found. Four decades later, Rothschild and Jordan (1903) described the predicted hawkmoth. According to Kritsky (1991), yet another species of *Angraecum* orchid with still deeper nectar has surfaced, and yet another hawkmoth with a still longer tongue has been predicted! Although pollination literature often focuses on comparative lengths of tongues and nectar tubes, which makes one think of coevolution, no general mechanism has been advanced to explain the diversity and evolution of hawkmoth tongue length.

Hawkmoth visitors at flowers are often known by plant taxa because so much knowledge of nectar foraging comes from pollination studies. Hawkmoths insert their tongues, sometimes more of their bodies, into blossoms for nectar. In the process, they touch pollen-bearing anthers and pollen-receiving stigmas, accidentally transferring pollen within or among blossoms. The extensive foraging range (Linhart & Mendenhall

1977), swift, darting flight, and nocturnal activity of many hawkmoths makes it more practical for an investigator to remain near flowers and observe arrivals, rather than follow such fleeting matchmakers to see what flowers they visit. Fluorescent powders, dyes, devices that enhance night vision, and palynological analysis of tongues and faces of captures have enhanced hawkmoth investigations of interest in the present study (Eisikowitch & Galil 1971, Kislev et al. 1972, Linhart & Mendenhall 1977, Haber & Frankie 1989). Some of the pollinator lists by plant taxa that include hawkmoths are those for *Angraecum* spp. (Nilsson et al. 1985), *Lavandula* sp. (Labiatae) (Herrera 1989), *Luehea* spp. (Tiliaceae) (Haber & Frankie 1982), *Pancratium maritimum* L. (Amaryllidaceae) (Eisikowitch & Galil 1971), and Polemoniaceae spp. (Grant & Grant 1965). Conversely, lists by hawkmoth species of plant taxa visited or pollinated (Fleming 1970, Kislev et al. 1972) are less common.

From lists of pollinators by plant taxa, seven pollinator syndromes—flower types favoring different animal pollinator groups—have been characterized, one being the syndrome of sphingophilous or hawkmoth flowers (Baker & Hurd 1968, Faegri & van der Pijl 1979). Sphingophilous flowers have the following traits: nocturnal anthesis or opening, white or pale coloration, sweet fragrance, horizontal to pendant posture, abundant sucrose-rich nectar, and long nectar tube (Baker & Hurd 1968, Faegri & van der Pijl 1979, Cruden et al. 1983, Haber & Frankie 1989). The nectar tube may be formed by various flower parts such as corolla, calyx, petal spur, hypanthium, or consist of a false tube formed by stamens and petals (Grant 1983). Hawkmoth flowers belong to the evolutionarily advanced stereomorphic and zygomorphic types of angiosperm flowers (Leppik 1968, Crepet 1979).

A shorter tongue than tube usually prevents nectar extraction; a longer tongue than tube lessens pollen removal and pollination effectiveness. Most hawkmoths use a range of available tube lengths, and many hawkmoth flowers are pollinated by a range of pollinator types. Nevertheless, comparative lengths of hawkmoth tongues and nectar tubes of hawkmoth flowers still interest investigators (Gregory 1963–64, Grant & Grant 1965, 1983a, 1983b, R. B. Miller 1978, 1981, 1985, Haber & Frankie 1982, 1989, Herrera 1989, Grant 1983, Martinez del Rio & Búrquez 1986, Nilsson et al. 1985, Nilsson 1988, and others). Tube lengths of North American hawkmoth flowers range from nil to 175 mm, and tongue lengths of associated hawkmoth pollinators, from 23 to 138 mm, averaging 53 and 60 mm, respectively (Grant 1983). Corresponding statistics in a Costa Rican community are nil to 190 mm, and 10 to 200 mm, averaging 51 and 49 mm, respectively (Haber & Frankie 1989). The resulting tube-to-tongue ratios of 0.88 and 1.04 approximate those experimentally implicating current interactions as maintaining

long tubes and long tongues (Nilsson 1988). Relations between hawkmoth pollinators and plants range from strong one-to-one tongue- and tube-length mutualisms (Nilsson et al. 1985) to more general matches (Leppik 1968, Proctor 1978, Feinsinger 1983, Howe 1984, Bawa 1990).

Contrary to the popular image of long-tongued hawkmoths, several sphingid lineages have vestigial tongues and head musculature. Rudimentary tongues were well known by the time of Rothschild and Jordan (1903), and documented further by Hättich (1907), Mell (1922, 1940), Kernbach (1962), and Fleming (1968). Sphingidae are members of the suborder Glossata. One of the classical defining traits of Glossata is the presence of a functional proboscis (Kristensen 1984). Thus the hawkmoth ancestor had a functional tongue, and vestigial tongues in modern hawkmoths must be the result of reduction. Tongue shortening to 10 mm or less renders hawkmoths incapable of nectar foraging (Fleming 1968), but does not necessarily prevent them from drinking water (Kernbach 1962; Pittaway 1993:106). Although as many as one-fifth of hawkmoth species have shortened tongues and do not forage for nectar, interest in nonfeeding has been dwarfed by interest in nectar foraging. It seems unlikely that a coevolutionary hypothesis of tongue and tube lengths could account for tongue reduction and the order-of-magnitude range in tongue lengths from 2.5 mm in *Laothoe juglandis* (J. E. Smith) (Fleming 1968) to 280 mm in *Amphimoeca walkeri*.

Life-system investigations of sphingids often involve either adult or immature stages, seldom both. One reason is that foodplants of the adult and immature stages usually differ. Comparison of larval and adult foodplant records shows that only 3 to 5 percent of hawkmoth species are known to use even one foodplant genus in both stages (Fleming 1970, Hodges 1971, Grant 1983, Pittaway 1993). Clues to hawkmoth tongue-length diversity and evolution have never been sought in any but the adult stage, nor at broader than local geographic scales.

Here I investigate tongue length on a continental spatial scale using large samples of both New World and Old World hawkmoth species. I explore correlations of tongue length with three variables: midrange latitude of hawkmoth distributions, growth-form of larval foodplants, and percentage of eggs that are mature at adult eclosion. I compare tongue length and tube length of hawkmoth flowers on a latitudinal gradient. Using comparative methodology, I test statistical significance of correlations of tongue length with larval-foodplant growth form, and chart the evolution of both traits as well as that of their correlation.

MATERIALS AND METHODS

In comparative studies, conventional parametric methods may inflate degrees of freedom in significance testing. The reason is that traits of interest may have been inherited from a common ancestor rather than evolved independently by each sample taxon. This

problem is addressed by phylogenetic nested analysis of variance and covariance (Bell 1989, Harvey & Pagel 1991). In nested analysis, values for a given trait are nested hierarchically. Here, for a trait like tongue length, populations are nested within species, species within genera, genera within tribes, and tribes within subfamilies. In nesting by taxonomic level, species represent population ancestors, genera represent species ancestors, tribes represent genus ancestors, and subfamilies represent tribe ancestors. Nested groups are not weighted here by number of subtaxa. I use conventional parametric statistics to introduce and describe correlations, and nested analysis to estimate independent evolution and test statistical significance.

Three kinds of correlation are involved in this study. First is conventional product-moment correlation, r estimating degree of association between a dependent variable and one independent variable, R when there are two independent variables. Product-moment correlation coefficients are usually not tested for significance here because of the degrees-of-freedom problem. The second kind of correlation is intrinsic correlation (Bell 1989), which is identical to variance-component correlation in the output of nested analysis. The intrinsic correlation coefficient estimates degree of association between two variables at various taxonomic levels, and resolves the degrees-of-freedom problem in significance testing. The third kind of correlation is intra- and interclass correlation. Intraclass correlation is the cumulative percentage of total variance at successively lower taxonomic or nesting levels. It is readily derived from variance components in the output of nested analysis. The intraclass correlation coefficient is used in this study to estimate independent evolution of a trait at a given taxonomic or nesting level, and to trace the geologic history of variation in the trait (Bell 1989). Finally, interclass correlation is the cumulative covariance or joint variation between two traits at successively lower taxonomic or nesting levels standardized by the geometric mean of cumulative variances for each trait (Bell 1989). The interclass correlation coefficient is used in this study to trace the geologic history of covariation between two traits (Bell 1989). Coefficients of product-moment correlation range strictly between 0 and 1, those of intrinsic, intra- and interclass correlation nominally between 0 and 1. I used the NESTED procedure of SAS (1988) to perform nested analyses.

My use of hawkmoth classification rather than phylogeny for nesting is necessary because a cladistic or modern hawkmoth phylogeny is not available. Classifications and phylogenies are not necessarily isomorphic, and nesting based on classification may obscure phylogenetic divergences intermediate between taxonomic levels (Harvey & Pagel 1991). The importance of obscured divergences, if any, will only be revealed when a modern phylogeny can be used in place of the classification. Hawkmoth classification has long been stable, which makes it a suitable surrogate for phylogeny. The classification dates from Rothschild and Jordan's (1903) landmark revision of the world fauna which has not been appreciably altered except at the subgeneric level, a level I omit in nesting. Tribes *Choerocampini* and *Macroglossini* have been synonymized under the latter name (Hodges 1971, Pittaway 1993), and I follow the resulting arrangement. For New World hawkmoths, nomenclature follows Hodges (1983) and D'Abrera (1986), in that order of preference. For Old World hawkmoths, nomenclature follows Pittaway (1993) and D'Abrera (1986), in that order of preference. I do not distinguish named infraspecific forms in this study except as populations. My geological time scale (Fig. 5) depicts taxonomic divergence in Sphingidae as very slow. Although inspired by Wilson (1978a, 1978b), the scaling is but a guess. Even if wrong in absolute time, however, it is accurate in relative time.

Population tongue length refers to different tongue measurements for a species from different parts of its range. Multiple reports of tongue length are available for 41% (29/70) of the New World sample of hawkmoth species (Appendix 1), and for 11% (9/81) of the Old World sample (Appendix 2). With one exception, species tongue lengths refer to single reports or arithmetic means of population values including both sexes; genus tongue lengths refer to arithmetic means of the means of constituent species; and tribe tongue lengths refer to arithmetic means of the means of constituent genera. The exception concerning species tongue lengths involves the correlation between percentage of eggs that are mature at adult eclosion and tongue length. In this correlation, species tongue lengths are from females only. Sexual dimorphism in hawkmoth tongue lengths is minor, and is

usually related to sexual dimorphism in body size. In the sample where only female tongue lengths are used, females average 2.0 mm longer tongues than males, ranging in individual species up to 5.9 mm longer ($n = 18$; species with tongue length >4.0 mm; Mell 1922).

New World tongue lengths (Appendix 1) are taken from Gregory (1963–64), Fleming (1968, 1970), Hodges (1971), R. B. Miller (1978, 1981, 1985), Bullock and Pescador (1983), Grant (1983), Grant and Grant (1983a, 1983b), Martinez del Rio and Búrquez (1986), and Haber and Frankie (1989). Old World tongue lengths (Appendix 2) are taken from Hättich (1907), Künckel d'Herculais (1916), Mell (1922, 1940), Kernbach (1961), Kislev et al. (1972), Nilsson (1983, 1988), Herrera (1989), and Pettersson (1991).

All published tongue lengths known to me for hawkmoths with midrange latitudes of 0° or greater northward are included in this study, except one set from Costa Rica (Young 1972). These appear discrepant. For example, tongue lengths reported for species of *Xylophanes* are about twice those for the same species elsewhere in Costa Rica and in western Mexico (Bullock & Pescador 1983, Haber & Frankie 1989). Similar differences occur in *Manduca*, *Eumorphia*, *Cocytius*, *Erinnyis*, *Pachylia*, and others.

Tongue length takes two forms in this study: arithmetic and natural logarithmic (\ln). I use \ln values in the nested analyses to homogenize variance (Bullock & Pescador 1983), and to place differences through a wide range on one scale. Arithmetic values appear in scattergrams, but are plotted on logarithmic scales. Scattergram trend lines are ordinary least-squares fits of the exponential function $y = a(10^x)$. I add 1 to latitudes and oogenesis percentages in some scattergrams and analyses to avoid computational and display problems associated with zero values. Flower-tube length also takes arithmetic form in description, and \ln form in analysis.

I use forewing length as a surrogate for body size. Live body-weight increases as the square of forewing length, which makes forewing length a sensitive index of body size (W. E. Miller 1997). Forewing lengths of sample New World hawkmoths are taken from Bullock and Pescador (1983); D'Abrera (1986), whose life-size illustrations of spread specimens I measured; and Haber and Frankie (1989). Forewing lengths of sample Old World hawkmoths are taken from Mell (1922) and D'Abrera (1986). In checking for body-size influence on tongue length, I examine the correlation between tongue length and forewing length at the genus rather than species level. Many hawkmoth species have common ancestry, which, as mentioned, may reduce the validity of significance testing at the species level. In checking for body-size influence on correlations between tongue length and larval foodplant growth-form, I divide sample species by forewing length into small, medium, and large aliquots. The respective forewing-length class limits for the New World sample are 17–35, 36–50, and 51–88 mm; and for the Old World, 14–29, 30–39, and 40–71 mm.

Midrange latitudes serve here as comparative indexes of hawkmoth distributions. Midrange latitude for a species is the latitude midway on a polar axis between north and south extremes of the breeding distribution of combined infraspecifics, excluding erratic records. For a genus, midrange latitude is the arithmetic mean of midrange latitudes of constituent species, and for a tribe midrange latitude is the arithmetic mean of mean midrange latitudes of constituent genera. Midranges of New World species (Appendix 1) are based on Schreiber (1978). Midranges of Old World species (Appendix 2) are based mostly on Mell (1922) and Pittaway (1993), sometimes on D'Abrera (1986).

Larval foodplant records for New World sample hawkmoths are from Hodges (1971), one source cited therein, and Janzen (1984); those for the Old World, from Mell (1922), Lin (1987), Pittaway (1993), and Chen (1994). Foodplants are truncated to genus, and non-native foodplant genera are excluded.

Larval foodplant growth-form index (Appendices 1, 2) refers to the typical height of mature plants and their associated size and tendency to dominate sites. Of several available growth-form classifications, I use a simple one similar to that in Janzen (1984), which recognizes five classes: tree, 25 m high; treelet, 10 to 25 m high; large-shrub, 5 to 10 m high; small-shrub, 3 to 5 m high; and herb (Grime 1979, Collinson 1988). Except for climbing foodplants, I numerically score growth forms according to Box (1981): 2 for herbs, 3 for small shrubs, 4 for large shrubs, 5 for treelets, and 6 for trees. Climbers are usually considered to have a growth-form value of zero, but here they receive values rang-

TABLE 1. Nested analysis of variance and covariance for tongue length (ln) and larval foodplant growth-form index. The subfamily level is omitted because of only two taxa at that level. Double asterisks indicate significance at $P < 0.01$.

Taxonomic (nesting) level	Variance					
	n	df	Tongue length	Growth form	Covariance	Intrinsic correlation
New World						
Tribe	5	3	0.580	0.667	-0.389	-0.63
Genus	34	29	0.474	0.707	-0.363	-0.63**
Species	70	36	0.083	1.282	-0.148	-0.45**
Population	124	54	0.008	0.000	0.000	0.00
Total	—	123	1.145	2.656	-0.519	-0.39**
Old World						
Tribe	4	2	0.467	0.420	-0.489	-1.10
Genus	38	35	0.380	0.352	-0.082	-0.22
Species	81	42	0.062	0.294	-0.037	-0.28
Total	—	80	0.909	2.212	-0.987	-0.70**

ing from 2 to 4 depending on size, whether woody or herbaceous, and whether annual or perennial, because they may be nearly as high and large as their plant supports (Janzen 1975). I obtained growth-form information from standard botanical compendia: for New World foodplants from Fernald (1950), Croat (1978), SCS (1982), and Janzen (1984); for Old World foodplants from Li (1935), Tutin et al. (1964, 1968), and Keng et al. (1993). Because many hawkmoth species use larval foodplants in several genera, foodplant growth-form values for species are usually means. The range of values underlying the mean growth-form for a hawkmoth is usually narrow, such as in Costa Rican hawkmoths (Janzen 1984). For a hawkmoth genus, foodplant growth-form index is the arithmetic mean of growth-form indexes of constituent species, and for a tribe, the arithmetic mean of growth-form indexes of constituent genera.

Data concerning percentage of eggs that are mature at adult eclosion are taken from Mell (1922, 1940). He recorded tongue length and numbers of mature and immature eggs and oocytes in 4 to 46 newly eclosed females per species in Old World hawkmoths (Appendix 2). He verbally described the resulting relation. I elaborate his observations with product-moment correlation analysis at species, genus, and tribe levels.

RESULTS

The assembled New World tongue-length sample consists of 124 observations on 70 species in 34 genera, 5 tribes, and 2 subfamilies, with multiple observations on 24 species (Table 1, Appendix 1). Although nesting extended to subfamily, no subfamily results are given for any variable because of only two taxa at that level. Tongue length in the New World sample varies inversely with latitude of midrange distribution at species, genus, and tribe levels, with product-moment correlation coefficients ranging between -0.44 and -0.57 (Fig. 1). Although these correlation coefficients were not tested for significance, they are judged to reflect a real relation because of similar signs and values at the different taxonomic levels. At the species level, mean tongue lengths at north latitudes of 0° (northern Brazil), 20° (southern Mexico), and 40° (central U. S.) are 50, 25, and 15 mm, respectively.

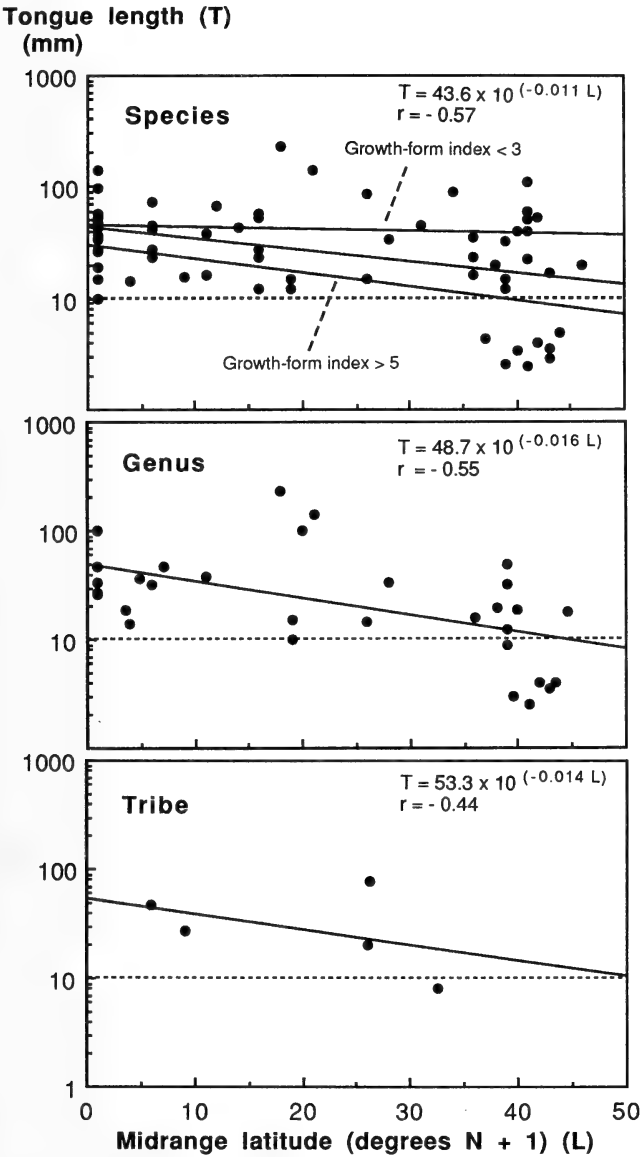


FIG. 1. Relation of tongue length to midrange latitude in New World hawkmoths at species, genus, and tribe levels. Points are means except where only one tongue-length value is available. The species equation describes the center trend line and encompasses all species points. Significance values are omitted because of problematic degrees of freedom as explained in text. Dotted lines at 10 mm represent length below which tongues are believed to be nonfunctional.

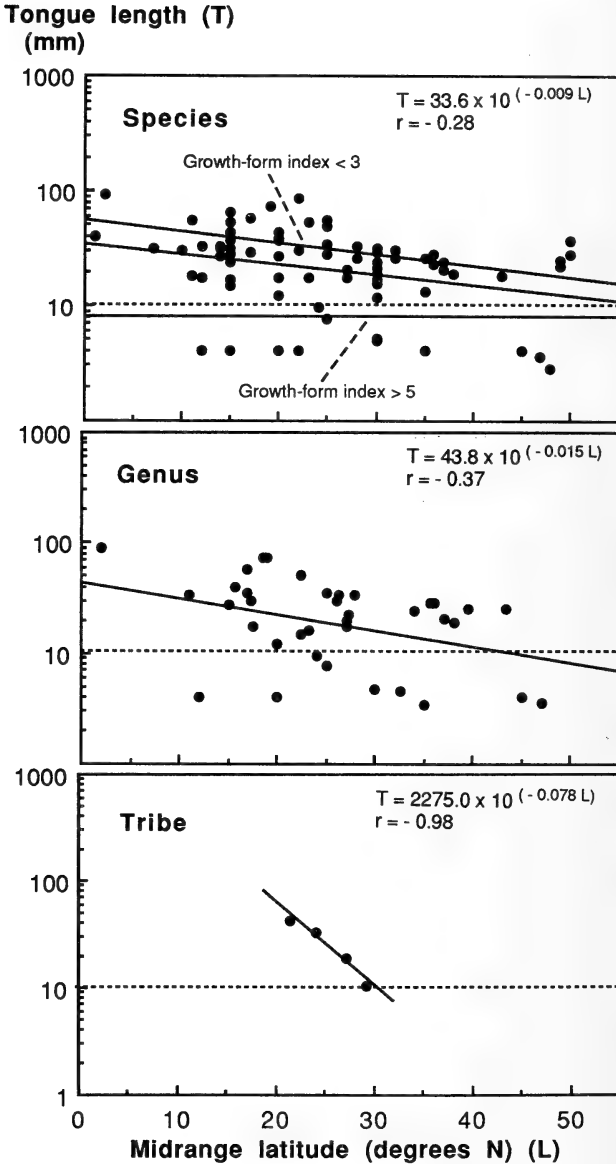


FIG. 2. Relation of tongue length to midrange latitude in Old World hawkmoths at species, genus, and tribe levels. Points are means except where only one tongue-length value is available. The species equation describes the center trend line and encompasses all species points. Significance values are omitted because of problematic degrees of freedom as explained in text. Dotted lines at 10 mm represent length below which tongues are believed to be nonfunctional.

The assembled Old World tongue-length sample consists of 92 observations on 81 species in 38 genera, 4 tribes, and 2 subfamilies, with multiple observations on 9 species (Table 1, Appendix 2). Although nesting extended to subfamily, no subfamily results are given for any variable because of only two taxa at that level. Old World tongue lengths also vary inversely with latitude of midrange distribution at species, genus, and tribe levels, with product-moment correlation coefficients ranging between -0.28 and -0.98 (Fig. 2). At the species level, mean tongue lengths at north latitudes of 0° (Borneo), 25° (southern China), and 50° (central Eurasia) are 42, 26, and 12 mm, respectively. The correlation here is also judged to reflect a real relation for the same reasons given above for the New World sample. New and Old World sample species represent 14% (151/1050) of the world hawkmoth fauna (D'Abrera 1986).

In both New and Old World tongue-length correlations with latitude, the trend lines for larval foodplant growth-form indexes <3 and >5 reveal a tendency for tongue lengths in these narrow index ranges to shorten as latitude increases (Figs. 1, 2). Thus the effect of latitude seems to operate regardless of foodplant growth-form.

Unlike tongue length, nectar-tube length appears to remain constant rather than shorten with increasing north latitude. In a community of hawkmoth flowers in Costa Rica (about 10° north latitude), mean tube length is 50 mm ($n = 30$; Haber & Frankie 1989), and in all known U. S. hawkmoth flowers (centering at 40° north latitude), mean tube length is 55 mm ($n = 124$; Grant 1983). The difference, 5 mm, is not significant ($P = 0.23$, Student *t*-test of difference in tube lengths [\ln]).

Tongue length is inversely correlated also with larval foodplant growth-form index at species, genus, and tribe levels. In the New World sample, the product-moment correlation coefficients range between -0.43 and -0.51 (Fig. 3). At the species level, mean tongue lengths at foodplant growth-form indexes of 2 (herbs), 4 (large shrubs), and 6 (trees) are 53, 27, and 14 mm, respectively. In the Old World sample, product-moment correlation coefficients range between -0.59 and -0.84 (Fig. 4). At the species level, tongue lengths at foodplant growth-form indexes of 2, 4, and 6 are 41, 17, and 8 mm, respectively. As before, these correlation coefficients were not tested for significance, but they are judged to reflect a real relation because of similar signs and values at the different taxonomic levels. The mean tongue lengths for a given growth-form index vary some between New and Old World samples, but the relations are similar in form.

Previous authors report significant correlations between tongue length and body size in local hawkmoth assemblages (Bullock & Pescador 1983, Haber & Frankie 1989). Investigation here reveals that positive correlations between tongue length (T) and body size (F) are

**Tongue length (T)
(mm)**

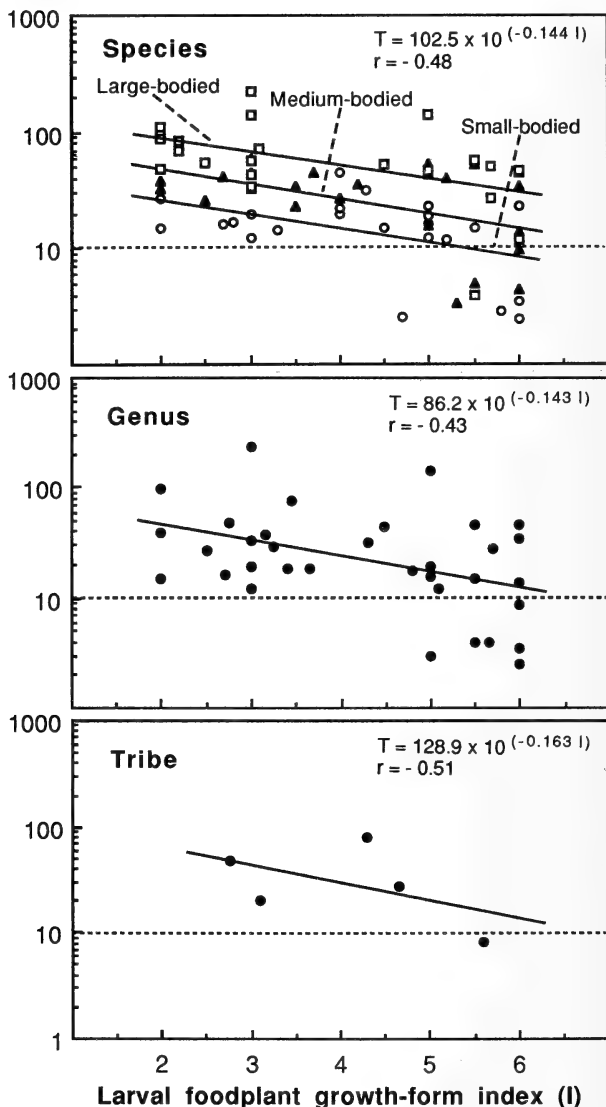


FIG. 3. Relation of tongue length to larval foodplant growth-form in New World hawkmoths at species, genus, and tribe levels. Points are means except where only one tongue-length value is available. The species equation represents all body sizes. Small, medium, and large body-size classes are defined, respectively, by forewing lengths of 17–31 mm (open circles), 32–46 mm (triangles), and 50–88 mm (open squares). Respective equations and product-moment correlation coefficients are $T = 45.0 \times 10^{-0.123 I}$ ($r = -0.45$), $T = 86.0 \times 10^{-0.128 I}$ ($r = -0.51$), and $T = 152.2 \times 10^{-0.117 I}$ ($r = -0.51$). Significance values are omitted because of problematic degrees of freedom as explained in text. Dotted lines at 10 mm represent length below which tongues are believed to be nonfunctional.

**Tongue length (T)
(mm)**

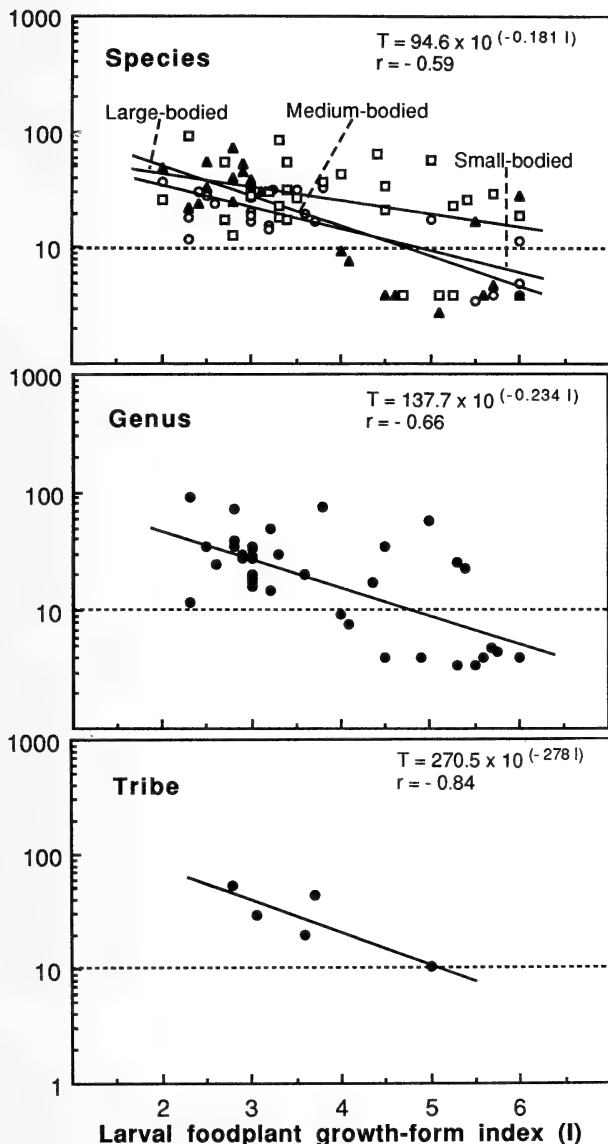


FIG. 4. Relation of tongue length to larval foodplant growth-form in Old World hawk-moths at species, genus, and tribe levels. Points are means except where only one tongue-length value is available. The species equation represents all body sizes. Small, medium, and large body-size classes are defined, respectively, by forewing lengths of 14–29 mm (open circles), 30–39 mm (triangles), and 40–71 mm (open squares). Respective equations and product-moment correlation coefficients are $T = 79.8 \times 10^{-0.1861 I}$ ($r = -0.78$), $T = 165.0 \times 10^{-0.2581 I}$ ($r = -0.76$), and $T = 69.1 \times 10^{-0.1121 I}$ ($r = -0.34$). Significance values are omitted because of problematic degrees of freedom as explained in text. Dotted lines at 10 mm represent length below which tongues are believed to be nonfunctional.

pervasive both above the species level and at broader geographic scales. For genera, the New World sample yields $T = 4.52 \times 10^{0.018F}$ ($r = 0.61$, $n = 34$); the Old World sample, $T = 7.53 \times 10^{0.011F}$ ($r = 0.32$, $n = 38$). If the degrees-of-freedom problem is assumed to be small at the genus level, then the significance values for these product-moment correlations are $P < 0.01$ and 0.05 , respectively.

Despite the influence of body size on tongue length, the tongue-length correlations with foodplant growth-form are not merely an outcome of different hawkmoth body sizes. Tongue length decreases in all body-size ranges as foodplant growth-form index increases. In the three body-size aliquots of New World species, product-moment correlations range between -0.49 and -0.58 , compared with -0.48 for all New World species (Fig. 3); in the three body-size aliquots of Old World species, they range between -0.34 and -0.78 , compared with -0.59 for all Old World species (Fig. 4). The most telling evidence that growth form operates in all body-size ranges is that regression slopes in all six New and Old World aliquots are negative. Multiple regression analysis echoes this conclusion in its standardized slope coefficients, which reveal the relative influence of independent variables (SYSTAT 1992). These coefficients for foodplant growth-form and body size in New World species are -0.44 and 0.61 , respectively ($r = 0.77$); and in Old World species -0.65 and 0.32 , respectively, ($r = 0.67$).

Similarity of tongue-length change with latitude and larval foodplant growth-form index at three taxonomic levels (Figs. 1–4) suggests not only real relations, but relations with a long history. Both suggestions are confirmed for growth-form index by nested analyses (Table 1, Fig. 5), and for latitude by extension and inference. Overall intrinsic correlations between tongue length and growth-form index for New and Old World hawkmoth samples are -0.39 and -0.70 , respectively ($P < 0.001$) (Table 1). Similar intrinsic correlations appear at the tribe level, which represents truly ancient ancestors. The respective New and Old World tribe covariances of -0.389 and -0.489 are the highest of any taxonomic level (Table 1). The histories of variation in tongue length and foodplant growth-form, as well as that of their covariation, show little change since genera diverged perhaps 15 million years before present (Fig. 5). Despite tongue-length relations with latitude and larval foodplant growth-form, it must be acknowledged that significant tongue-length variation remains unexplained (Figs. 1–4, Table 1).

The sample concerning percentage of eggs that are mature at adult eclosion in relation to tongue length consists of 26 Old World species in 14 genera, 2 tribes, and 1 subfamily (Appendix 2). Mell (1940) concluded from this sample that oogenesis at adult eclosion is more advanced the shorter the tongue. Mell's conclusion also applies at the

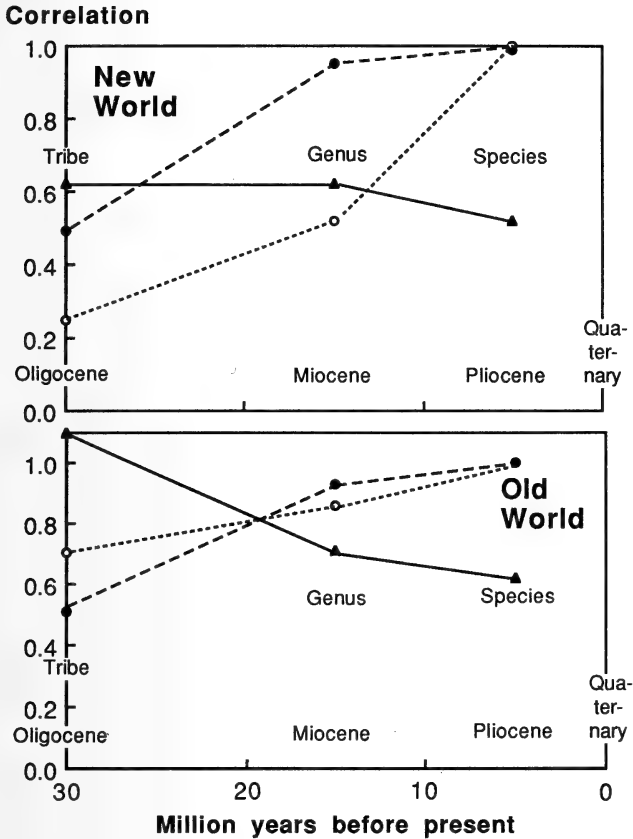


FIG. 5. Evolution of tongue length (solid circles, dashed lines), larval-foodplant growth-form (open circles, dotted lines), and their covariation (triangles, solid lines) at different taxonomic levels. Points for tongue length and foodplant growth-form represent intraclass correlations, and points for covariation represent interclass correlations, as explained in text. The geologic time scale is a best guess based on Wilson (1978a, b).

genus level, and, as far as the data go, at the tribe level (Fig. 6). These results point to another ancient relation. At the species level, mean percentage of eggs mature at eclosion for tongue lengths of 20, 50, and 80 mm, are 30, 15, and 7, respectively. If total egg production were known and incorporated, it would probably intensify the relation. That is, in long-tongued individuals, oocytes undetected at adult eclosion, or formed afterwards, would likely grow and mature from resources gained by nectar foraging. The link between tongue length and reproductive readiness at adult eclosion confirms that tongue length is intimately involved in hawkmoth life-system evolution.

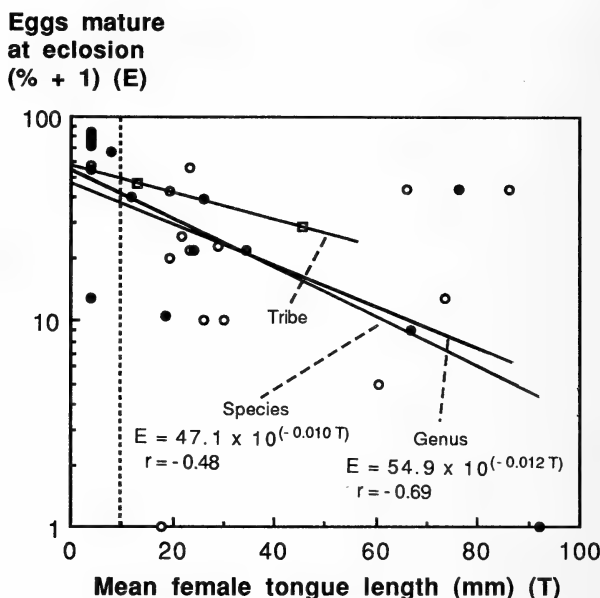


FIG. 6. Relation of egg maturity at eclosion to tongue length in Old World hawkmoths. Points are means for females. Closed circles represent species, open circles genera, and open squares tribes. Data from Mell (1922, 1940). Dotted line at 10 mm represents length below which tongues are believed to be nonfunctional.

DISCUSSION

A hypothesis of hawkmoth tongue-length diversity and evolution must account for both tongue lengthening and shortening as well as for the new findings in this study. I summarize these findings as follows. Mean tongue length decreases with increasing north latitude worldwide (Figs. 1, 2), whereas tube length of hawkmoth flowers appears to remain constant. Mean tongue length decreases with increasing larval food-plant growth-form index worldwide (Figs. 3, 4, Table 1). Further, the shorter the tongue, the greater the percentage of eggs that are mature at adult eclosion (Fig. 6). These relations are ancient, their trends having formed before the divergence of genera, postulated as occurring in middle Miocene time, some 15 million years before present (Fig. 5).

At least three-quarters of the 25 tree genera used as larval foodplants by hawkmoths in this study are recorded as fossils from the middle Miocene or earlier (Leopold & MacGinitie 1972, Tanai 1972, Vakhrameev 1991). Also, plants with stereomorphic flowers, or still more advanced zygomorphic flowers with long nectar tubes, existed by the middle Miocene also (Leppik 1968, Proctor 1978, Crepet 1979). Thus the

**No. phanerogam
species locally (N)**

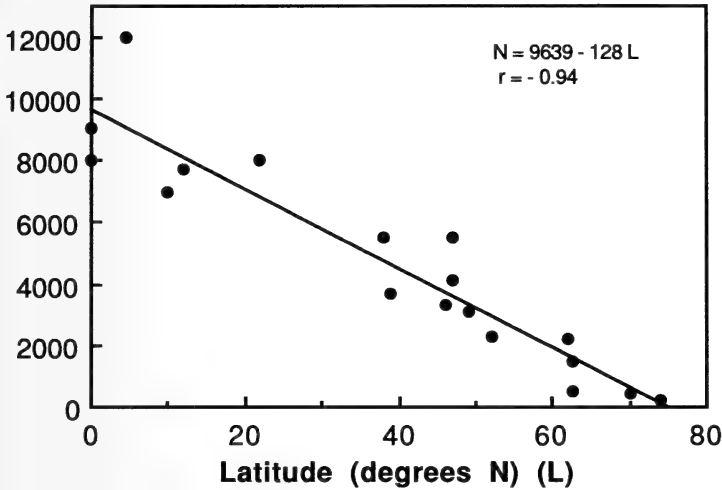


FIG. 7. Species richness of local seed-plant floras in the northern hemisphere as related to latitude. Data from Rejmánek (1976).

potential for larval foodplants of high growth-form index, and adult foodplants with long-tubed flowers, to influence tongue length seems easily coextensive with the history of tongue-length variation on the postulated geologic time scale (Fig. 5). The latitudinal gradient in tongue length is equally or more ancient; the position of the continents relative to the equator has not changed greatly since the Paleocene, some 60 million years before present (Smith & Briden 1977).

No doubt many plausible hypotheses of tongue length diversity and evolution could be given. I favor an admittedly anthropocentric possibility, which focuses on larval foodplant finding, a process that remains to be studied. Especially in extratropical landscapes, herb foodplants (growth-form index 2) may be harder to find than tree foodplants (growth-form index 6). Moreover, foodplants of any growth-form index may be easier to find at higher north latitudes today because there is little doubt that patch size increases with increasing north latitude. This increase in patch size is as yet poorly quantified, and can best be visualized as a function of the polar-equatorial gradient of species richness in plants (Fig. 7). In this gradient, the number of seedplant species in local floras decreases at higher latitudes worldwide (Rejmánek 1976, Currie & Paquin 1987). As floras diminish in species richness toward polar regions—from near 10,000 species at the equator to one-fifth that num-

ber in central North America and central Eurasia (Fig. 7)—woody plants, and probably vascular plants in general, may occur in larger stands or patches (Dobzhansky 1950, Bourgeron 1983, Longman & Jeník 1987). Tropical forests often contain 60 to 1000 tree species per ha. In such forests, it seems physically impossible for very many individuals of one kind of tree to occur contiguously. Although unclear whether patch size of all plant growth-forms in the tropics would be similarly affected, small patch size for trees seems likely to prevail. In contrast, temperate forests often have only one or a few tree species per ha, rarely more than 10, and large patch sizes for trees and other plant growth-forms prevail.

Most hawkmoth adults are heavy bodied, and their energy expenditure in flight is enormous, with hovering consuming about 1 mg of sugar g^{-1} body weight min^{-1} (Heinrich 1983). For hawkmoths that must find nonpersistent, inconspicuous foodplants of low growth form in small patches (Figs. 2, 4, 7), and whose eggs are mostly immature at eclosion (Fig. 6), long tongues and nectar foraging are essential. The longer the tongue, the greater and faster the access to nectar in flowers of different depths, and the greater the chances of mutualistic specialization (Nilsson 1988, Haber & Frankie 1989, Herrera 1989). Also, the deeper the nectar, the more of it plants produce (Haber & Frankie 1989). In contrast, long tongues and nectar foraging may be superfluous for hawkmoths that have the easy task of finding persistent, conspicuous larval foodplants of high growth form in large patches (Figs. 2, 4, 7), and whose eggs are mostly mature at eclosion (Fig. 6).

The association of tongue shortening and larval feeding on trees in Glossata is not unique to hawkmoths (W. E. Miller 1996). Larvae of *Lymantriidae* and *Saturniidae* feed almost exclusively on trees or other woody plants, and their adults do not feed (Ferguson 1971–72, 1978, Janzen 1984, Schaefer 1989, Stone 1991). The same is true for many subgroups in other families such as *Geometridae*. Another trait associated with larval tree-feeding and loss of adult feeding capability in some Glossata is reduction in female flight capability. Flightless females dramatically demonstrate that flight is not essential when larval foodplants are trees occurring in large stands or patches (Gohrbandt 1940, Barbosa et al. 1989, Sattler 1991).

Although the foregoing speculative hypothesis involves mechanisms operating at continental geographic scales, it does not rule out other mechanisms of tongue-length adjustment operating at local scales.

ACKNOWLEDGMENTS

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APPENDIX 1. Taxa and variable values for sample New World hawkmoths. Sources are given in the Methods section. For mean tongue length, values without decimals are single observations in a single report; values with decimals are means of multiple observations at one location; values with decimals and SD are means of observations at multiple locations enumerated by (n).

Species	Mean tongue length \pm SD (mm)	Midrange latitude (°N)	Mean larval foodplant growth form index
Sphinginae: Sphingini			
<i>Agrius cingulata</i> (F.)	99.2 \pm 4.6 (4)	0	2.0
<i>Cocytius antaeus</i> (Drury)	139	20	5.0
<i>Ceratomia amyntor</i> (Gey.)	12.0	38	6.0
<i>C. catalpae</i> (Bdv.)	4.4	36	6.0
<i>C. undulosa</i> (Wlk.)	9.8	40	6.0
<i>Dolba hyloeus</i> (Drury)	32	38	4.3
<i>Lapara bombycoides</i> Wlk.	3.5	42	6.0
<i>Manduca barnesi</i> (Clark)	52.0	15	4.5
<i>M. corallina</i> (Drc.)	56.8 \pm 1.6 (2)	15	5.5
<i>M. dilucida</i> (Hy. Edw.)	43.2 \pm 0.4 (2)	13	5.0
<i>M. florestan</i> (Cram.)	72.0 \pm 15.6 (3)	5	3.1
<i>M. lefeburei</i> (Guér.)	51.8 \pm 1.2 (2)	0	5.0
<i>M. muscosa</i> (R. & J.)	86.0	25	2.2
<i>M. quinquemaculata</i> (Haw.)	110.0 \pm 14.9 (4)	40	2.0
<i>M. occulta</i> (R. & J.)	68.0	11	2.2
<i>M. rustica</i> (F.)	138.3 \pm 5.1 (3)	0	3.0
<i>M. sexta</i> (L.)	89.0 \pm 6.4 (4)	33	2.0
<i>Neococytius chluentius</i> (Cram.)	228.5 \pm 37.5 (2)	17	3.0
<i>Sphinx chersis</i> (Hbn.)	50.4 \pm 7.6 (5)	40	5.7
<i>S. drupiferarum</i> J. E. Sm.	52.0 \pm 11.3 (2)	41	5.5
<i>S. eremitoides</i> Stkr.	39.0	40	2.0
<i>S. kalmiae</i> J. E. Sm.	40	39	5.2
<i>S. libocedrus</i> Hy. Edw.	45	30	4.0
<i>S. sequoiae</i> Bdv.	23.0	35	6.0
<i>S. vashiti</i> Stkr.	60.0 \pm 2.6 (3)	40	3.0
Sphinginae: Smerinthini			
<i>Laothoe juglandis</i> (J. E. Sm.)	2.5	40	6.0
<i>Pachysphinx modesta</i> (Harr.)	4.0	41	5.5

APPENDIX 1. Continued.

Species	Mean tongue length \pm SD (mm)	Midrange latitude (°N)	Mean larval foodplant growth form index
<i>Paonias excaecatus</i> (J. E. Sm.)	3.4	39	5.3
<i>P. myops</i> (J. E. Sm.)	2.6	38	4.0
<i>Protambulyx strigilis</i> (L.)	27.5 \pm 0.7 (2)	0	5.7
<i>Smerinthus cerisyi</i> Kirby	5	43	5.5
<i>S. jamaicensis</i> (Drury)	2.9	42	5.8
Macroglossinae: Dilophonotini			
<i>Aellopos clavipes</i> (R. & J.)	16.0	10	5.0
<i>A. fadus</i> (Cram.)	15.0	0	4.5
<i>A. titan</i> (Cram.)	23.0	5	5.0
<i>Callionima falcifera</i> (Gehl.)	15.5 \pm 0.7 (2)	8	5.0
<i>Erinnyis alope</i> (Drury)	44.8 \pm 0.2 (2)	5	3.7
<i>E. ello</i> (L.)	36.0 \pm 1.0 (3)	0	4.2
<i>E. lassauxii</i> (Bdv.)	40.8 \pm 1.6 (2)	5	2.7
<i>E. obscura</i> (F.)	27.0 \pm 1.4 (2)	5	2.0
<i>Eupyrrhoglossum sagra</i> (Poey)	19.0	0	5.0
<i>Hemaris diffinis</i> (Bdv.)	17.0	42	2.8
<i>H. thysbe</i> (F.)	19.4	45	4.0
<i>Isognathus rimosus</i> (Grt.)	34.2 \pm 1.1 (2)	27	6.0
<i>Nyceryx coffeae</i> (Wlk.)	14	3	6.0
<i>Pachylia ficus</i> (L.)	46.5 \pm 0.7 (2)	0	5.0
<i>P. syces</i> (Hbn.)	45.0 \pm 0.0 (2)	0	6.0
<i>Pachylioides resumens</i> (Wlk.)	26.5 \pm 0.7 (2)	0	2.5
<i>Perigonia lusca</i> (F.)	15.0	18	5.5
<i>Phryxus caicus</i> (Cram.)	33	0	3.0
<i>Pseudosphinx tetrio</i> (L.)	46.5 \pm 3.5 (2)	0	6.0
Macroglossinae: Phillampelini			
<i>Eumorpha achemon</i> (Drury)	45.7 \pm 3.8 (3)	0	3.0
<i>E. anchemola</i> (Cram.)	58.0	0	3.0
<i>E. fasciata</i> (Sulz.)	48.0	0	2.0
<i>E. labruscae</i> (L.)	55.0	0	2.5
<i>E. pandorus</i> (Hbn.)	34.5	35	3.0
<i>E. vitis</i> (L.)	42.9 \pm 0.1 (2)	0	3.0
Macroglossinae: Macroglossini			
<i>Amphion floridensis</i> Clark	16.0	35	2.7
<i>Cautethia spuria</i> (Bdv.)	12.0	18	5.2
<i>C. yucatana</i> Clark	12.3	15	5.0
<i>Darapsa myron</i> (Cram.)	14.7	38	3.3
<i>D. pholus</i> (Cram.)	22	40	4.0
<i>Deidamia inscripta</i> (Harr.)	12.2	38	3.0
<i>Hyles lineata</i> (L.)	38.3 \pm 1.5 (11)	10	2.0
<i>Proserpinus terlooii</i> Hy. Edw.	14.8	25	2.0
<i>Sphecodina abbottii</i> (Swain.)	19.5	37	3.0
<i>Xylophanes phuto</i> (F.)	34.5 \pm 0.7 (2)	0	3.5
<i>X. porcus</i> (Hbn.)	27.5 \pm 0.7 (2)	15	4.0
<i>X. tersa</i> (L.)	33.5 \pm 2.1 (2)	0	2.0
<i>X. turbata</i> (Hy. Edw.)	23.0 \pm 1.4 (2)	15	3.5

APPENDIX 2. Taxa and variable values for sample Old World hawkmoths. Sources are given in the Methods section. For mean tongue length, values with decimals are means of multiple observations from one location; values with decimals and SD's are means of observations from multiple locations enumerated by (n). Superscript b = species used here in the correlation between percentage of eggs that are mature at adult eclosion and tongue length (Fig. 6). Superscript c = tongue so short as to be nonfunctional according to Mell (1922, 1940); mean of all nonfunctional tongues measured by him was assigned.

Species	Mean tongue length \pm SD (mm)	Midrange latitude (°N)	Mean larval foodplant growth form index
Sphinginae: Sphingini			
<i>Acherontia atropos</i> (L.)	13.0	35	2.8
<i>A. lachesis</i> (F.) ^b	17.6 \pm 1.8 (2)	12	3.4
<i>A. styx</i> (Westw.) ^b	17.7 \pm 1.1 (2)	23	2.7
<i>Agrius convolvuli</i> (L.) ^b	90.9	2	2.3
<i>Dolbina inexacta</i> (Wlk.) ^b	7.6	25	4.1
<i>Meganoton analis</i> (Fldr.) ^b	56.5	17	5.0
<i>M. rufescens</i> Btlr. ^b	72.5	—	—
<i>Psilogamma increta</i> (Wlk.) ^b	63.7	15	4.4
<i>P. menephron</i> (Cram.) ^b	84.6	22	3.3
<i>Sphinx calligineus</i> Btlr. ^b	11.6	30	6.0
<i>S. ligustri</i> L.	36.6	50	3.8
<i>S. pinastri</i> L.	28.5 \pm 1.4 (2)	50	6.0
Sphinginae: Smerinthini			
<i>Ambulyx kuangtungensis</i> (Mell)	17.0	30	5.5
<i>A. liturata</i> Btlr. ^b	29.7	30	5.7
<i>A. ochracea</i> Btlr. ^b	21.6	30	4.5
<i>A. schauffelbergeri</i> B. & G. ^b	19.0	30	6.0
<i>A. sericeipennis</i> Btlr. ^b	25.8	28	5.4
<i>A. subocellata</i> Fldr. ^b	23.5	15	5.2
<i>Amplipterus panopus</i> (Cram.) ^b	34.6	12	4.5
<i>Clanis bilineata</i> (Wlk.) ^b	22.9	36	3.3
<i>C. undulosa</i> Moore ^b	26.2	32	2.0
<i>Cypa decolor</i> Wlkr. ^b	4.0 ^c	12	6.0
<i>Laothoe populi</i> (L.)	4.0 \pm 1.4 (2)	45	5.6
<i>Leucophlebia lineata</i> Westw.	9.5	24	4.0
<i>Marumba cristata</i> (Btlr.) ^b	4.0 ^c	15	5.2
<i>M. dyras</i> (Wlk.) ^b	4.0 ^c	15	4.7
<i>M. gaschkewitschi</i> (B. & G.) ^b	4.0 ^c	35	4.6
<i>M. spectabilis</i> (Btlr.) ^b	4.0 ^c	15	5.1
<i>Mimas tiliae</i> (L.)	3.5 \pm 0.7 (2)	47	5.5
<i>Parum colligata</i> (Wlk.) ^b	4.8	30	5.7
<i>Polyptychus trilineatus</i> Moore ^b	4.0 ^c	20	4.5
<i>Smerinthulus chinensis</i> R. & J. ^b	4.0 ^c	22	5.7
<i>S. pallidus</i> Mell	5.0	30	6.0
<i>Smerinthus ocellatus</i> (L.)	2.8 \pm 0.4 (2)	48	5.1
<i>S. planus</i> Wlk. ^b	4.0 ^c	35	6.0
Macroglossinae: Dilophonotini			
<i>Cephonodes hylas</i> (L.)	20.1	27	3.6
<i>Hemaris staudingeri</i> (Leech)	20.6	37	3.0
<i>Sataspes infernalis</i> (Westw.)	16.9	15	3.7
<i>S. tagalica</i> Bdv.	17.5	20	5.0

APPENDIX 2. Continued.

Species	Mean tongue length \pm SD (mm)	Midrange latitude (°N)	Mean larval foodplant growth form index
Macroglossinae: Macroglossini			
<i>Acosmerycoides leucocraspis</i> (Hamp.)	27.9	15	3.0
<i>Acosmeryx castanea</i> R. & J.	30.4	32	3.1
<i>A. naga</i> (Moore)	32.0	30	3.4
<i>A. pseudomissa</i> Mell	27.5	20	3.5
<i>A. sericeus</i> (Wlk.)	30.2	22	3.2
<i>Ampelophaga rubiginosa</i> B. & G.	28.2	36	3.0
<i>Aspledon himachala</i> (Btlr.)	15.4	30	3.2
<i>A. hyas</i> (Wlk.)	14.6	15	3.2
<i>Cechenena lineosa</i> (Wlk.)	55.3	25	3.4
<i>C. minor</i> (Btlr.)	44.2	20	2.9
<i>Daphnis hypothous</i> (Cram.)	43.5	15	4.0
<i>Deilephila elpenor</i> (L.)	21.9 \pm 0.6 (3)	49	2.3
<i>D. porcellus</i> (L.)	18.5 \pm 0.3 (2)	43	2.3
<i>Hayesiana triopus</i> (Westw.)	33.0	28	3.0
<i>Hippotion boerhaviae</i> (F.)	31.4	7	3.5
<i>H. rafflesi</i> (Btlr.)	37.0	15	2.0
<i>Hyles gallii</i> (Rtmbg.)	25.4 \pm 0.6 (3)	49	2.8
<i>H. livornica</i> (Esper)	24.4	30	2.4
<i>Macroglossum bombylans</i> (Bdv.)	28.0	25	2.5
<i>M. corythus</i> Wlk.	33.3	14	3.0
<i>M. passalus</i> (Drury)	32.3	12	3.8
<i>M. pyrrhostictum</i> (Btlr.)	31.4	15	3.0
<i>M. sitiene</i> (Wlk.)	31.8	7	3.2
<i>M. stellatarum</i> (L.)	26.4	35	2.0
<i>M. troglodytus</i> (Bdv.)	26.9	14	3.0
<i>Micracosmeryx macroglossoides</i> Mell	17.2	27	3.0
<i>Panacra busiris</i> Wlk.	38.4	20	3.0
<i>P. mydon</i> Wlk.	32.0	14	3.0
<i>Pergesa actea</i> (Cram.)	73.5	19	2.8
<i>Rhagastis albomarginatus</i> (Roths.)	29.2	17	3.0
<i>R. mongoliana</i> (Btlr.)	24.0	37	2.6
<i>R. olivaceae</i> (Moore)	49.5	25	2.0
<i>Sphingonaepiopsis pumilio</i> (Bdv.)	12.0	20	2.3
<i>Sphecodina caudata</i> (B. & G.)	18.9	38	3.0
<i>Theretra alecto</i> (L.)	52.7	23	2.9
<i>T. clotho</i> (Drury)	18.5	11	3.3
<i>T. japonica</i> (Orza)	27.7	36	3.0
<i>T. latreillei</i> (MacLeay)	40.2	1	2.8
<i>T. nessus</i> (Drury)	55.5	11	2.7
<i>T. oldenlandiae</i> (F.)	32.8	14	2.5
<i>T. pallicosta</i> (Wlk.)	37.2	20	3.0
<i>T. silhetensis</i> (Wlk.)	30.5	10	2.4
<i>T. suffusa</i> Wlk.	53.9	15	2.5

THE IDENTITY OF *FILATIMA ORNATIFIMBRIELLA*
(CLEMENS 1864) (GELECHIOIDEA: GELECHIIDAE)

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ABSTRACT. Adults of *Filatima ornatifimbriella* (Clemens 1864) can be confused with three other species, two of which, *Filatima occidua* and *Filatima adamsi* are new. *Filatima ornatifimbriella* (Clemens) and *F. xanthuris* (Meyrick) are redescribed, and complete synonymy for each species is given. A lectotype is designated for *Gelechia amorphaeella* Chambers 1877. Photographs of wing patterns and scanning electron micrographs of diagnostic wing features are included. A key to the species is provided in conjunction with illustrations of male and female genitalia.

Additional key words: Lepidoptera, Gelechiidae, *Filatima*, *ornatifimbriella*.

Classifications based on single character systems often result in recognition of polyphyletic groups. More natural classifications at the species and generic levels for Lepidoptera result when genital characters are analyzed together with head and venational characters. This realization by previous lepidopterists enabled them to recognize *Gelechia* Hübner as a composite taxon and prompted a transfer of species from this concept to existing or newly recognized genera (Busck 1939, Sattler, 1960). *Filatima* (Busck 1939) was recognized as a result of these observations.

Filatima is characterized as follows: labial palpus recurved to near vertex, third segment nearly as long as second segment, anteroventral scales of second segment divergent, forming a "furrowed brush;" ocellus present; forewing with M_2 , M_3 , and CuA_1 somewhat approximate; hindwing with M_3 and CuA_1 connate; R_s and M_1 approximate; male hindwing often with curtain scaling (Busck 1939 ["curtain scales"]; Clarke 1947 [curtain scaling]) within area from wing base to slightly beyond end of cell and between $Sc+R_1$ and R_s (Figs. 8–9), other sex scales on posterior half of discal cell and basal portion of cells M_3-CuA_1 and CuA_1-CuA_2 , and part of anal area (Figs. 8–10); male genital capsule enclosed within eighth segment; uncus hood shaped; gnathos narrow and somewhat recurved; costal lobe of valva elongate and narrow; saccular lobe of each valva asymmetric; vinculum rounded; aedeagus with lateral sclerite from zone and several other internal sclerites; ventral surface of eighth tergum with paired, basolateral scale pencils, dorsal surface usually with prominent, long, anteriorly directed scales arising posteromedially; female genitalia with antrum sclerotized or membranous; inception of ductus seminalis on anterior part of accessory bursa; posterior

part of corpus bursae and accessory bursa often with dense microtrichia; signum present or absent.

Most *Filatima* are Holarctic in distribution with the greatest species' diversity in semiarid areas of western United States and Mexico. Their larvae are leaf tiers on *Acacia* Mill., *Amorpha* L., *Astragalus* L., *Cercidium* Tul., *Glycyrrhiza* L., *Leucaena* Benth., *Lupinus* L., *Mimosa* L., *Prosopis* L., *Robinia* L., *Thermopsis* Robt. Brown, *Vicia* L. (Fabaceae); *Prunus* L., *Purshia* DC. (Rosaceae); *Ribes* L. (Saxifragaceae); *Vaccinium* L. (Ericaceae); *Phoradendron* Nutt. (Loranthaceae); *Salix* L. (Salicaceae); and *Betula* L. (Betulaceae) (host information taken from specimen label data on material in USNM collection).

The closely similar wing patterns of *Filatima ornatifimbriella* (Clemens) and *F. xanthuris* (Meyrick) have led to their being misidentified in museum collections as well as confused with the other species described herein. The goals of this study are to clarify the taxonomic relationships among these species and to provide efficient means for their identification.

METHODS

The *Methuen Handbook of Colour* (Kornerup & Wanscher 1978) was used as a color standard for the description of the adult vestiture. Genitalia were dissected as described by Clarke (1941), except mercurochrome and Chlorazol Black E (Kodak) were used as stains. In addition, the ventral part of the genital capsule was separated from the dorsal part so both aspects could be examined with minimal distortion and confusion related to overlap (Fig. 15 contrasted with Figs. 16–18), following Pitkin (1984) and Huemer (1987). Terminology of genitalia follows Klots (1970). Pinned specimens and genital preparations were examined with stereoscopic and compound microscopes. Wing measurements were made using a hand-held micrometer. Specimens for SEM studies were mounted on stubs using double-sticky tape and coated with gold-palladium for five minutes with a HUMMER-X sputter coater. Wing scale ultrastructure was studied using an AMRAY 1810 Scanning Electron Microscope.

RESULTS

Key to the Species of *Filatima* Confused with *F. ornatifimbriella*

1. Male 2
- Female 4
2. Valval saccular lobes slightly asymmetrical (Fig. 16) *ornatifimbriella*
- Valval saccular lobes greatly asymmetrical (Figs. 17–18) 3
3. Lateral sclerite from zone projected from aedeagus, curved, ventral sclerite subelliptical, without a serrate edge (Fig. 20) *xanthuris*
- Lateral sclerite from zone not projected from aedeagus, straight; ventral sclerite subtriangular, with a serrate edge (Fig. 21) *adamsi*

4. Antrum sclerotized, signum present (Figs. 22, 24) 5
 - Antrum membranous, signum absent (Fig. 23) *xanthuris*
 5. Membrane adjacent to anterior apophyses forming a deep invaginated pocket,
 microtrichia within (Fig. 22) *ornatifimbriella*
 - Membrane adjacent to anterior apophyses not forming an invaginated pocket,
 without microtrichia (Fig. 24) *occidua*

Filatima ornatifimbriella (Clemens 1864)

(Figs. 1, 11–12, 16, 19, 22)

Gelechia ornatifimbriella; Clemens 1864:420; Chambers 1878b:145; Smith 1891:102; Dyar 1903:517; Busck 1903:899; Barnes & McDunnough 1917:157; Forbes 1923:271; Meyrick 1925:84; McDunnough 1939:71.

Filatima ornatifimbriella; Hodges 1983:23.

Gelechia unctulella; Zeller 1873:257–8; Chambers 1878b:147; Smith 1891:102; Dyar 1903:513; Busck 1903:878; Barnes & McDunnough 1917:157 [jr. syn. of *ornatifimbriella*]; Forbes 1923:267; Meyrick 1925:84 [jr. syn. of *ornatifimbriella*]; McDunnough 1939:71 [jr. syn. of *ornatifimbriella*]; Busck 1939:575 [jr. syn. of *ornatifimbriella*].

Gelechia xanthuris; McDunnough 1939:72 [misident.].

Filatima xanthuris; Busck 1939:576 [misident.].

Gelechia amorphaeella; Chambers 1877:124; Chambers 1878a:111; Chambers 1878b:141; Smith 1891:100; Dyar 1903:516; Barnes & McDunnough 1917:158; McDunnough 1939:71.

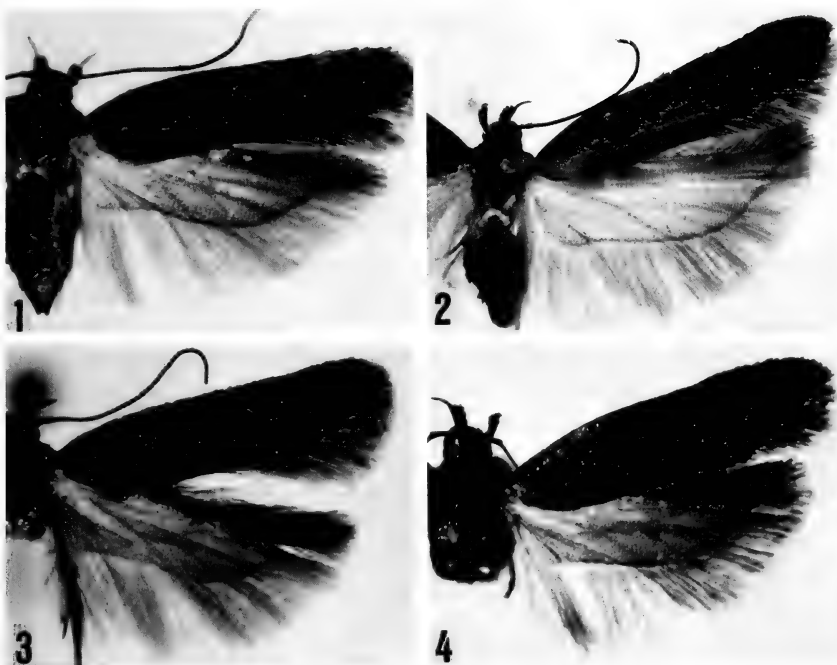
Filatima amorphaeella; Busck 1939:575; Hodges 1983:23, [jr. syn. of *ornatifimbriella*].

Gelechia amorphella; Busck 1903:891 [missp., unrecognized]

Gelechia amorphella; Meyrick 1925:84 [emend.].

Diagnosis. Gnathos hooklike apically, costal lobe of valva produced slightly beyond saccular lobe, saccular lobe narrow, posterior margin of vinculum entire, lateral sclerite of aedeagus spinose and medially twisted, dorsal lobe truncate apically, ventral part of antrum with two subequal ribbonlike sclerites, posterior part of corpus bursae with dense microtrichia, signum small, dentate. Most specimens of *ornatifimbriella* can be recognized by the large circular discal spots and the pale grayish-brown distal 1/5 of the forewing.

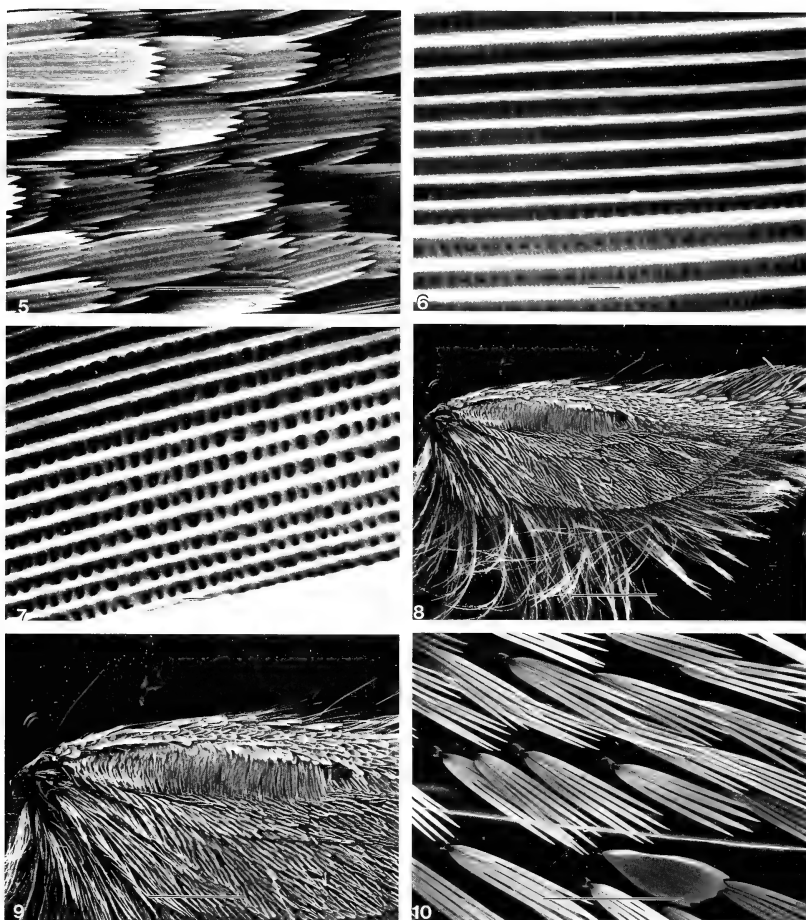
Description. *Head*: haustellum dark brown basally, pale grayish brown distally; maxillary palpus dark brown; dorsal and medial surfaces of labial palpus pale grayish brown, ventrolateral surfaces dark brown or scales pale brown basally, dark brown apically; vertex of second segment with individual scales pale grayish brown basally, brown or dark brown distally; frons with pale grayish-brown scales medially, dark-brown scales in front of eye; vertex and frons slightly darker than frons, scales with lustrous reflections, each scale gradually widened from base, apical margin entire, rounded, scales posterad of eye dark brown; antennal scape, pedicel, and a variable number of basal flagellomeres dark brown above, other flagellomeres with individual scales pale grayish brown basally, dark brown distally, antenna yellowish gray underneath. *Thorax*: mesonotum and tegula pale grayish brown intermixed with brown; lateral surface of legs mostly dark brown intermixed with pale grayish brown, tibiae with a narrow white band at 1/2 length and apex, apex of each tarsomere white, mesial surface white. *Forewing* (Fig. 1): length 6.5–8.5 mm ($n = 13$); most wing scales pale grayish brown basally, dark brown distally, each scale gradually widened from base, distal margin serrate (Fig. 5 of *F. xanthuris*); anterior margin of wing dark brown basally, becoming mottled dark brown and gray to 3/4 length, then pale grayish brown; a dark-brown subcircular spot at 3/5 length of cell and one at end of cell; discal spots large or small, equal or distal spot larger, separate or united; mid-discal spot absent in some specimens; scales on undersurface pale grayish brown basally, brown apically; anterior margin brown. *Hindwing*: male with one acanthus, female with two acanthi; upper surface pale grayish brown, darkening slightly to apex, undersurface pale gray/off-white, veins and margin of wing darker; undersurface of male with curtain scaling (Figs. 8–9 of *F. xanthuris*) from wing base to slightly beyond end of cell and between $Sc+R_1$ and R_s ; curtain scaling perpendicular to anterior margin, extending to near middle of cell; each



FIGS. 1–4. Species of *Filatima*. 1, female *F. ornatifimbriella* (Clemens); 2, male *F. xanthuris* (Meyrick); 3, holotype female of *F. adamsi*, n. sp.; 4, holotype male of *F. occidua*, n. sp.

scale elongate, with deeply dissected distal margin; male with pale-gray sex scales between veins posterad of curtain scaling to anal area (Figs. 8–10 of *F. xanthuris*). *Abdomen*: terga 1–6/7 with basal part grayish brown, distal margin white; sterna mostly pale grayish brown medially, brown laterally; male eighth tergum an invaginated pouch (Fig. 11), with piliform sex scales originating from anterolateral arms; male eighth sternum (Fig. 12) with two short anterolateral arms, distal emargination broad and rounded. *Male genitalia* (Figs. 16, 19): gnathos elongate, narrowed distally forming a recurved hook; costal lobe of valva narrow throughout length, setose, extending slightly beyond saccular lobe; saccular lobes nearly symmetrical, setose, strongly arched medially and curved dorsally at apex; posterior margin of vinculum entire; aedeagus with lateral sclerite from zone spinose, medially twisted, dorsal lobe (=sclerotized lobe from zone (Hodges 1986)) truncate apically, internal lobe longer than ventral lobe, and with broader distal margin. *Female genitalia* (Fig. 22): ovipositor with two telescopic membranous parts; posterior apophyses much longer than anterior apophyses; membrane adjacent to anterior apophyses forming a deeply invaginated pocket bearing microtrichia; antrum with two subequal, ribbonlike sclerites ventrally, one subtriangular and one oval sclerite dorsally; corpus bursae and accessory bursae with many hairlike microtrichia within posterior end; inception of ductus seminalis on anterior part of accessory bursae; signum heavily sclerotized, small, anterior margin finely dentate.

Types. *Gelechia ornatifimbriella* Clemens. Holotype: ♂; type no. 7347; “Ill[inois];” “♂ genitalia slide by RW Hodges, 2936” [Academy of Natural Sciences of Philadelphia, ANSP]. *Gelechia unctulella* Zeller. Holotype: ♂; “type 1703” [red label]; “Dallas, Tex[as], Boll” “Zeller.” “*Gelechia unctulella* Z[eller]” [handwritten, green label]; “♂ genitalia slide

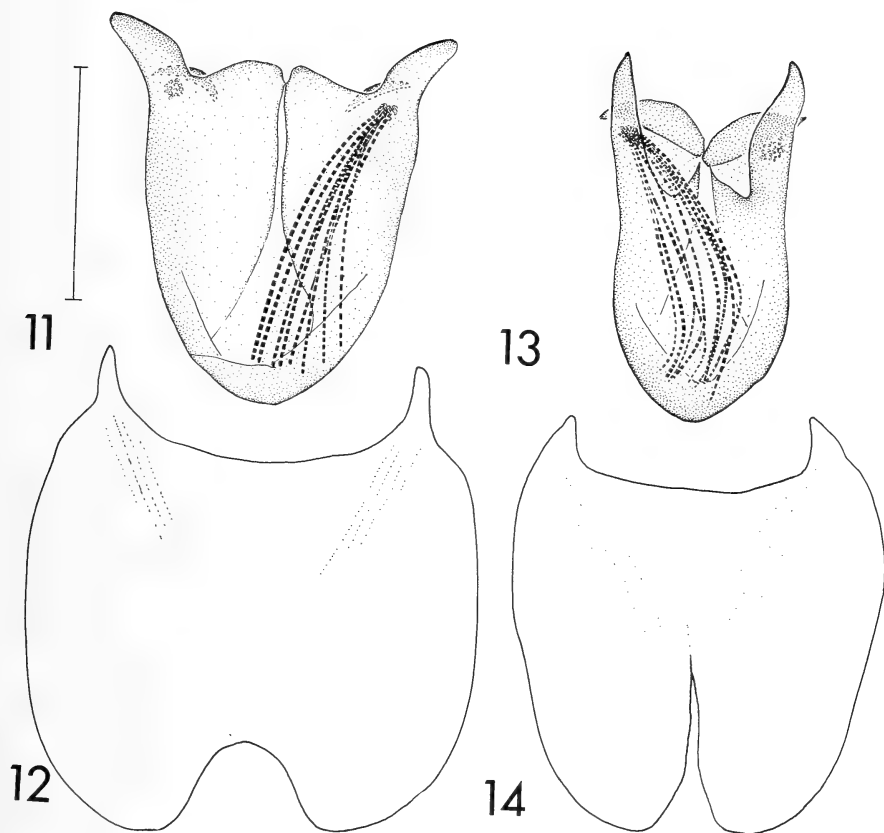


FIGS. 5-10. Ultrastructure of scales of *Filatima* fore- and hindwings. 5-6, scales of forewing of *Filatima xanthuris* (Clemens); 7, scales of forewing of *Filatima depuratella* (Busck); 8-9, hindwing of male *Filatima xanthuris* (Clemens) showing curtain scaling within area from wing base to slightly beyond end of cell; 10, highly dissected male sex scales within lower half of discal cell, basal part of cells M_3 - CuA_1 and CuA_1 - CuA_2 , and entire anal area. Line scale = 1.0 μ m for Figs. 5-7, 10; line scale = 1.0 mm for Figs. 8-9.

3285, RW Hodges." [Museum of Comparative Zoology, MCZ]. *Gelechia amorphaeella* Chambers. **Lectotype:** ♂; present designation; "Type 1480" [red label]; "Chambers, Color[ado]" "*Gelechia amorphaeella*, Cham[bers] Col[lection]" [handwritten label]; "Lectotype, RW Hodges" [handwritten label]; "♂ genitalia slide 3289, by RW Hodges." Lectotype and two paralectotypes, all with same label data, in MCZ. One specimen of syntype series apparently lost.

Foodplants. *Amorpha fruticosa* L. (Fabaceae) (Chambers 1878a and pinned specimens).

Distribution. *Filatima ornatifimbriella* is known from five localities: [Rock Island?], Illinois; Halsey, Nebraska; Edgerton, Colorado; Dallas, Texas; and Riverside, California.



FIGS. 11–14. Eighth tergum and sternum of *Filatima*. **11**, eighth tergum of *F. ornatifimbriella* (Clemens); **12**, eighth sternum of *F. ornatifimbriella* (Clemens); **13**, eighth tergum of *F. xanthuris* (Meyrick); **14**, eighth sternum of *F. xanthuris* (Meyrick). Line scale = 1.0 mm.

Adults have been reared from larvae (June–July). The species overwinters as an adult, based on specimen label data; but it does not appear to have been collected at light. Specimens examined: 5 ♂, 8 ♀, 8 slides.

Filatima xanthuris (Meyrick 1927)
(Figs. 2, 5–6, 8–10, 13–15, 17, 20, 23)

Gelechia xanthuris; Meyrick 1927:346; McDunnough 1939:72.

Filatima xanthuris; Hodges 1983:23 [revised status].

Gelechia ornatifimbriella; Clarke 1932:67, pl. 2, fig. 4 (male gen.), pl. 3, fig. 4 (female gen.) [misident.].

Filatima ornatifimbriella; Busck 1939:575, pl. 60, Figs. 11, 11a, 11b (male gen.), pl. 66, Fig. 44 (female gen.) [misident.]; Clarke 1969, 7:99, pl. 49, figs. 4, 4a, 4b (wing pattern, aedeagus, genital capsule), lectotype designation of *Gelechia xanthuris* Meyrick and treatment as junior synonym of *F. ornatifimbriella* [misident.].

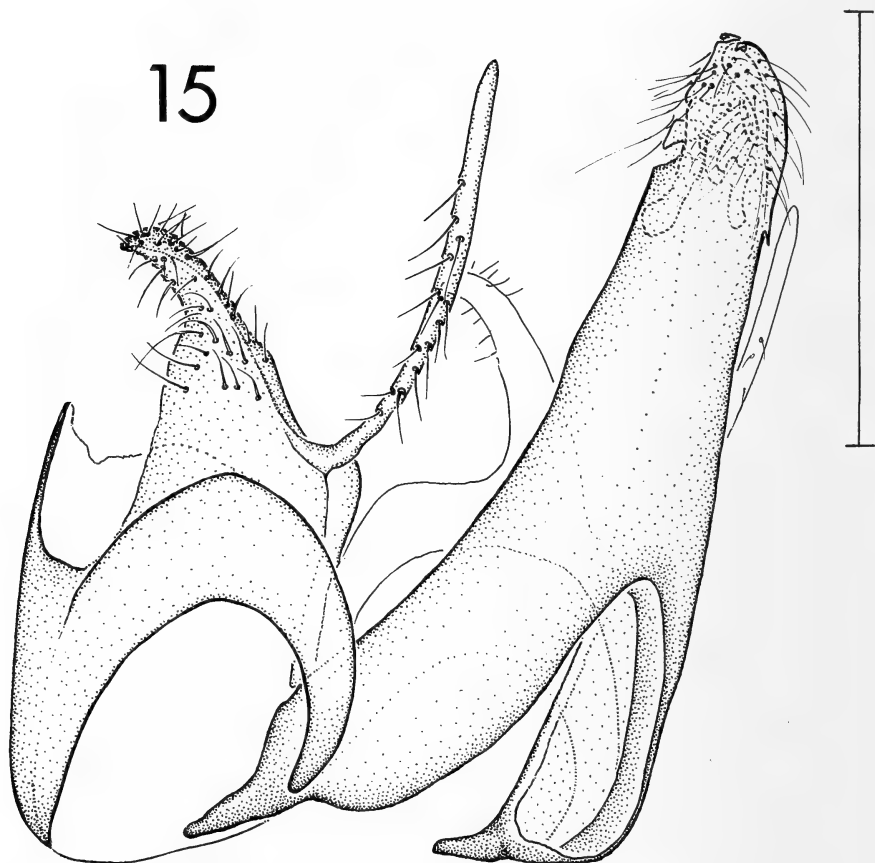
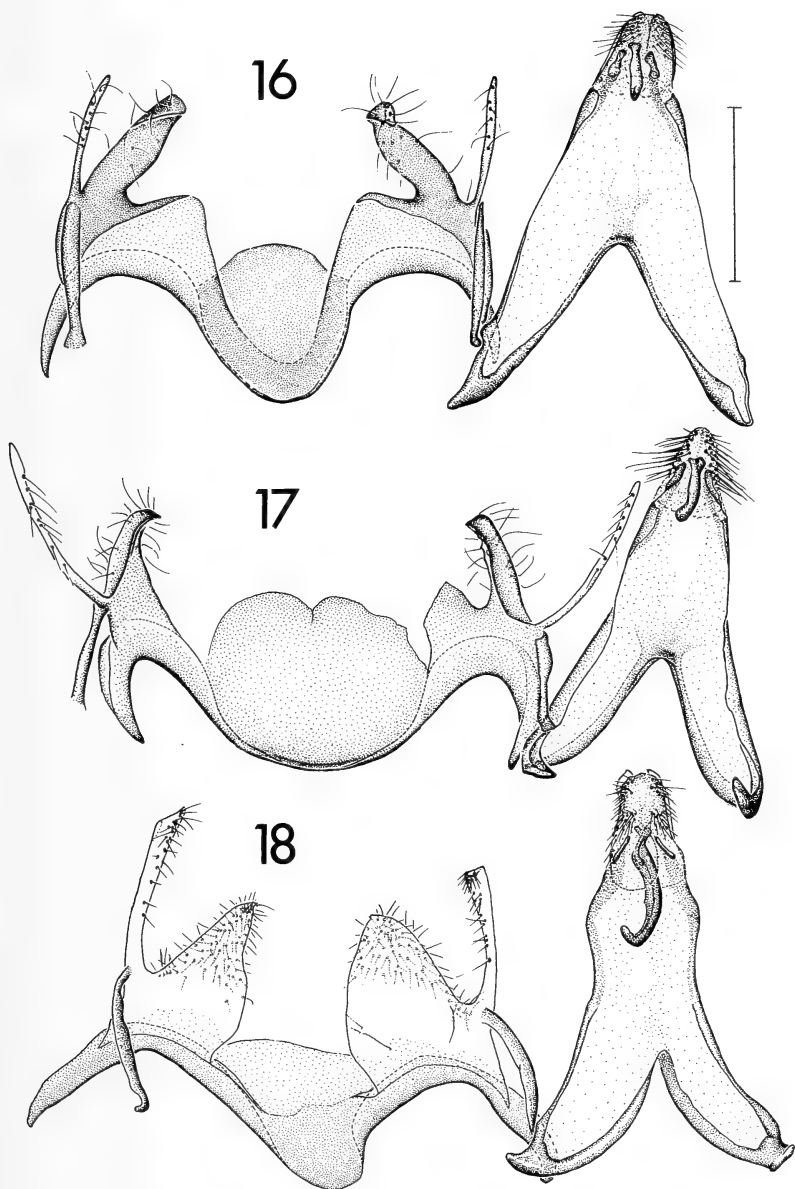


FIG. 15. Lateral view of male genitalia of *Filatima xanthuris* (Meyrick) with vinculum not separated from dorsal elements of genital capsule. Genital capsule rotated laterally 45 degrees. Line scale = 1.0 mm.

Diagnosis. Gnathos apically rounded and blunt, costal lobe of valva extending well beyond saccular lobe, inner surface of left saccular lobe with a broad and angular basal lobe, right saccular lobe slightly widened basally, posterior margin of vinculum slightly emarginate medially, aedeagus with lateral sclerite from zone fingerlike, dorsal lobe obtuse apically, internal lobe slightly longer and narrower than ventral lobe. Most specimens of *F. xanthuris* can be recognized by the united, subrectangular discal spots of the forewing.

Description. As for *F. ornatifimbriella* except: *Forewing* (Fig. 2): length 6.0–10.1 mm ($n = 208$); individual scales pale brownish gray basally, brown or dark brown distally; discal spots variable, usually subrectangular, large or small, subequal or unequal, separate or united; many specimens with various spots and/or streaks basal to spot at middle of cell; two short streaks along CuP (united in some specimens), one basal spot on midline of cell; one subcostal spot between spots at base of middle of cell; basal spots appear to be present or absent in any combination. *Abdomen*: male eighth tergum narrow (Fig. 13); distal margin of male eighth sternum deeply emarginate medially (Fig. 14). *Male genitalia* (Figs. 15, 17, 20): gnathos apically rounded and blunt; costal lobe of valva narrow throughout



FIGS. 16–18. Male genitalia of *Filatima*. **16**, male genitalia of *F. ornatifimbriella* (Clemens); **17**, male genitalia of *F. xanthuris* (Meyrick); **18**, male genitalia of *F. adamsi*, n. sp. Line scale = 1.0 mm.

length, setose, extending well beyond saccular lobe; saccular lobes asymmetrical, inner surface of left lobe with a broad and angular lobe, right lobe widened basally; posterior margin of vinculum slightly emarginate medially; aedeagus with lateral sclerite from zone fingerlike; apical margin of dorsal lobe obtuse; internal lobe slightly longer and narrower than ventral lobe. *Female genitalia* (Fig. 23): as for *F. ornatifimbriella*, except lobe adjacent to anterior apophyses slightly invaginated; antrum membranous.

Types. Lectotype: ♂, designated and figured by Clarke (1969), BM slide no. 5771, Dividend, Utah, 26 April. Lectotype and nine paralectotypes in The Natural History Museum, London, BM(NH).

Foodplants. *Thermopsis pinetorum* Greene, *Lupinus* sp., *Robinia* sp., *Vicia* sp. (Fabaceae) (pinned specimens).

Distribution. *Filatima xanthuris* has been collected in the mountains of North and South Carolina; the Boston Mountains, Arkansas; Tenkiller Lake, Oklahoma; Silverton, Colorado; Guadalupe Mountains, Texas; Lincoln County, New Mexico; Coconino County, Arizona; Utah County, Utah; Lander County, Nevada; Riding Mountains, Manitoba; Rocky Mountains in Alberta and British Columbia; generally in Washington; and Lincoln County, Oregon. Adults have been collected from 26 March to 10 October. Specimens examined: 96 ♂, 108 ♀, 68 slides.

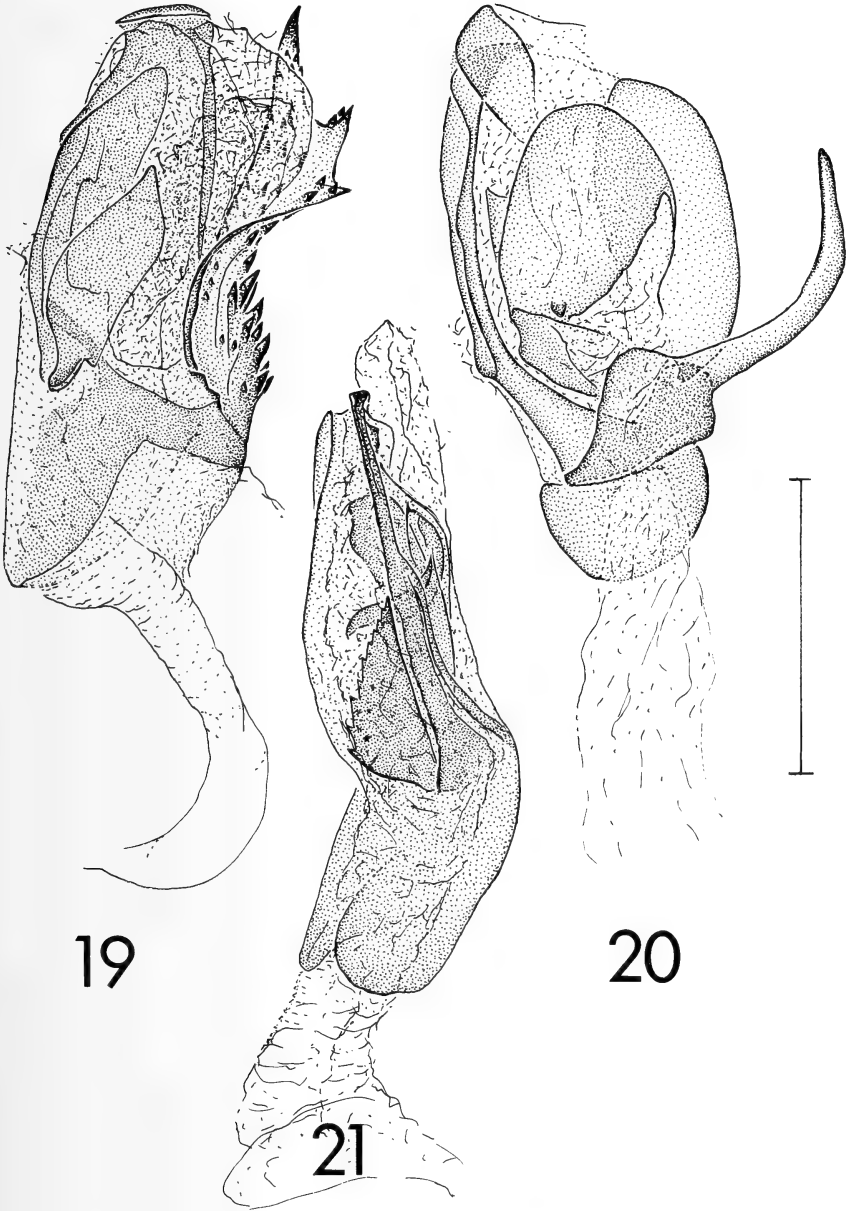
Remarks. Preliminary, comparative studies of the ultrastructure of the dorsal forewing scales of *F. xanthuris* and *F. depuratella* (Busck) indicate that *Filatima* with shiny scales have large windows between the longitudinal ridges of each scale, whereas *Filatima* with dull scales have either few smaller windows or no windows between longitudinal ridges (Figs 6–7).

Filatima adamsi Hodges & Adamski, new species

(Figs. 3, 18, 21)

Diagnosis. Frons with scales in front of eye generally concolorous with rest of frons, a few dark-brown scales present. Gnathos broadly curved, costal lobe of each valva slender, gradually widening from 2/5 length to apex, extending well beyond saccular lobe, saccular lobes of valvae asymmetrical, lobe of left valva with mesial margin broadly curved, lobe of right valva with mesial margin sinuous, becoming narrower apically; posterior margin of vinculum entire; aedeagus with sclerites as illustrated. Female genitalia unknown.

Description. *Head*: haustellum and maxillary palpus grayish brown basally, becoming pale grayish brown distally; labial palpus with first segment mainly dark gray brown laterally, second segment grayish orange dorsobasally, then brown almost to apex, apex and ventral scale tuft mottled pale and dark gray, scale tuft narrow, third segment mainly dark brown with scattered off-white scales; frons, vertex, and occiput mainly shining yellowish gray, individual scales darker at apices, scales on frons tipped with dark brown, several brown scales in front of eye, scales on vertex and occiput with small gray area at apex of each; scape and shaft of antenna mainly dark brown, ventral surface of scape yellowish gray, individual scales on shaft paler at base than apex, antenna broken after flagellomere 10/11; ocellus present. *Thorax*: mesonotum and tegula appearing gray brown, individual scales pale yellowish gray basally, gray brown distally; foreleg coxa mottled yellowish gray and gray brown, mainly dark, femur, tibia, and tarsus medium to dark gray brown, with pale scales just beyond 1/2 length of tibia and at apex, apex of tarsomeres 1–4 off-white; midleg similar to foreleg but slightly darker; hindleg unknown. *Forewing* (Fig. 3): length 7.0 mm (n = 1); mainly dark gray brown, individual scales paler at base; an irregular dark gray-brown mark at 3/5 length of cell, a dark gray-brown blotch at end of cell, several dark gray-brown scales along fold from near base to 3/4 length of fold, several pale-gray scales on anterior and posterior margins at 4/5 wing length, fringe on distal margin mainly pale gray, individual scales tipped darker gray. *Hindwing*: undersurface with curtain scales, additional sex scales extending from base of wing toward posterior margin and in the cell to vein 2A. *Abdomen*: upper surface with mostly pale grayish-brown scales intermixed with brown scales; undersurface mostly white mesially, mostly dark-brown scales intermixed with brown scales ventrolaterally; male eighth tergum most similar to that of *xanthuris*, sternum most similar to that of *ornatifimbriella*, except posterior margin less emarginate.



FIGS. 19–21. Male genitalia (aedeagi) of *Filatima* (for orientation note that the ductus ejaculatorius enters the aedeagus on the dorsal surface). **19**, aedeagus of *F. ornatifimbriella* (Clemens); **20**, aedeagus of *F. xanthuris* (Meyrick); **21**, aedeagus of *F. adamsi* n. sp. Line scale = 1.0 mm.

Male genitalia (Figs. 18, 21): vinculum asymmetric, saccus directed toward right; costal lobe of valva wider distally than at base, extending well beyond saccular lobe; saccular lobes asymmetrical, left lobe broad, right lobe narrower apically; posterior margin of vinculum entire; gnathos hook shaped, strongly curved in distal 1/3; aedeagus with several sclerotized flanges and plates on distal 1/2; a prominent, subtriangular plate with serrate lateral margin. **Female genitalia**: unknown.

Types. *Holotype*: ♂. Label data: "M[aine]: West P[oint], Little Wood Is[land], 13 Aug[ust] 1972, S. B. Adams leg." "♂ Genitalia slide by DA, USNM 87529" [green label]. Holotype in National Museum of Natural History, USNM.

Foodplants. Unknown.

Distribution. *Filatima adamsi* is known only from the type locality. It was collected at incandescent light.

Remarks. This species appears closely allied to *F. vaniae* Clarke by sharing similarly shaped costal lobes of the valvae and the aedeagus with a subtriangular ventral sclerite with a serrate edge. They differ in that *adamsi* has wider saccular lobes and longer costal lobes of the valvae. In addition, *vaniae* is paler. The hindlegs are missing on the holotype.

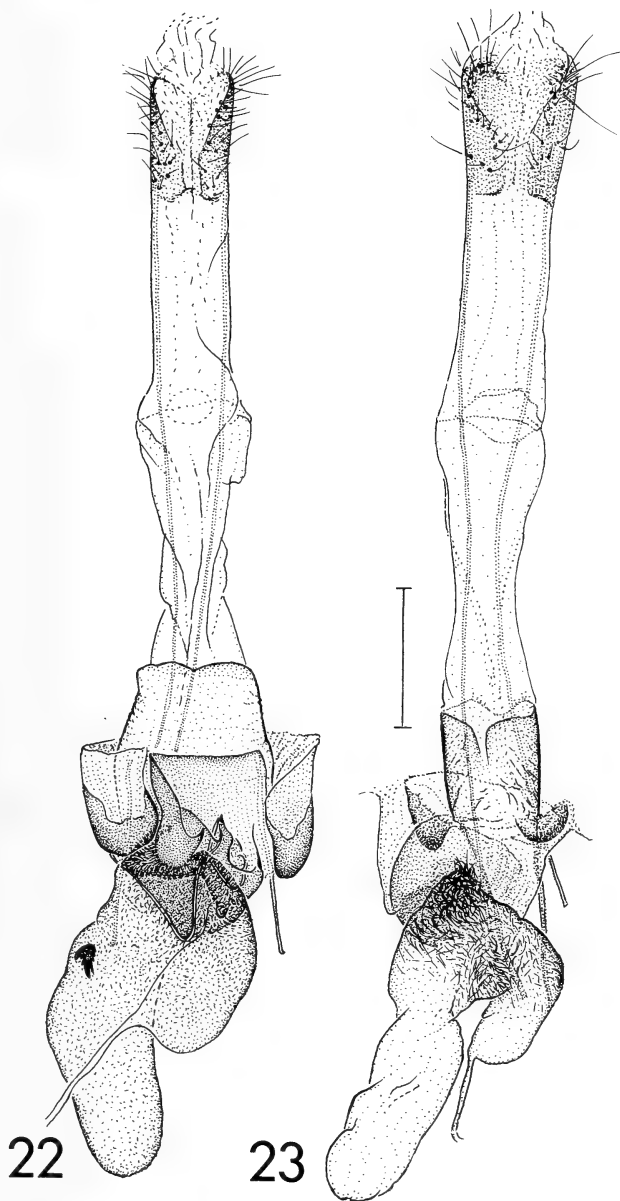
Etymology. This species is named after its collector, Mrs. Sally B. Adams (now Mrs. S. A. Brady).

***Filatima occidua* Hodges & Adamski, new species** (Figs. 4, 24)

Diagnosis. A small medium to dark-gray moth with a small dark-brown spot at 2/3 the length of the cell and an irregular dark-brown mark at the end of the cell on the forewing. Dorsodistal margin of antrum heavily sclerotized and broadly incurved mesially; antero-lateral margin of seventh abdominal sternum with a V-shaped invagination. Right lobe of corpus bursae with dense, fine spicules on basal 1/3; zone of spicules extending basomesially onto antrum. Signum with a pair of inwardly directed, triangular, lateral lobes; each lobe dentate, particularly on posterior margin.

Description. *Head*: maxillary palpus and base of haustellum dark brown, haustellum becoming yellowish brown by 1/2 length; labial palpus mainly brown, individual scales pale gray brown at extreme base of each scale, dorsomesial surface of second segment pale gray from base to 1/2–3/5 length, third segment mottled with many pale-gray/off-white scales, particularly on posterior margin; antenna mottled dark brown and pale gray/off-white, ventral surface of scape pale, most scales of shaft pale nearly to apices, distal margins very dark brown; frons, vertex, and occiput mainly shining pale yellowish gray, dark-brown scales in front of eye directed ventromesially and slightly overlapping on ventral part of frons, scales on vertex and occiput very narrowly margined with slightly darker gray; ocellus present. *Thorax*: tegula dark brown at base, yellowish gray distally, individual scales narrowly margined with darker gray, mesothorax mainly medium to pale gray, individual scales tipped and streaked darker gray; foreleg with coxa mottled dark brown and pale gray, individual scales streaked darker gray on distal 3/4, femur, tibia, and tarsus mainly brown, individual scales pale gray based, apex of each tarsomere with off-white scales; midleg similar to foreleg but surfaces generally paler, tarsomeres with many gray scales; hindleg as for midleg, mesial surface noticeably very pale gray/off-white. *Forewing* (Fig. 4): length 5.5–6.2 mm (n = 5): mainly dark gray, yellowish-brown tipped scales on basal 1/5, dark-gray tipped scales from 1/5–4/5 length and dark-brown tipped scales at apex, a brown spot at 3/5 length of cell and dark-brown blotch at end of cell. **Male genitalia**: unknown. **Female genitalia** (Fig. 24): salient features given in diagnosis.

Types. *Holotype*: ♀, "Pullman, W[ashington]n, J.F. Clarke, 3-VIII-[19]32"; "Reared from *Lupinus ornatus* [Douglas x Lindl.]; "3144"; "♀ genitalia slide by AB, USNM 9716" [green label]; "♀ genitalia slide by AB, Aug[ust] 30/[19]43" [handwritten label]. USNM. *Paratypes*: 3 ♀, "Mill Valley, Marin Co[unty], Cal[ifornia], IX-26-1925"; "H.H. Keifer, Collector"; "♀ genitalia slide by DA, USNM 87551" [green label]; "♀ genitalia slide by DA, USNM 87519" [green label]; one specimen not dissected; ♀, same data as above except, "February 4, 1926" ♀, "July 24–31". Paratypes in California Academy of Sciences, San Francisco and USNM.



FIGS. 22–23. Female genitalia of *Filatima*. 22, female genitalia of *F. ornatifimbriella* (Clemens); 23, female genitalia of *F. xanthuris* (Meyrick). Line scale = 1.0 mm.

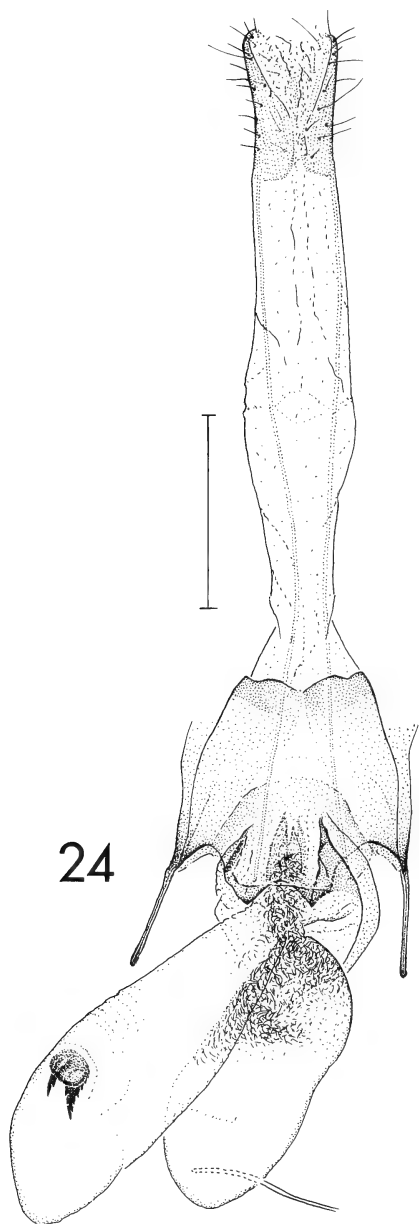


FIG. 24. Female genitalia of *Filatima occidua*, n. sp. Line scale = 1.0 mm.

Foodplants. *Lupinus sericeus* Pursh, var. *sericeus* (Fabaceae). Currently, *L. ornatus* Douglas x Lindl. is a junior synonym of *L. sericeus* Pursh, var. *sericeus*.

Distribution. *Fatima occidua* is known from southeastern Washington and Marin County, California. Adults have been collected on 4 February, 3 August, and 26 September.

Etymology. The specific epithet is derived from the Latin *occiduus*, -a, -um, meaning setting [of the sun] and referring to the distribution of *occidua*.

DISCUSSION

Comparison of the male and female genitalia suggest that the *Filatima* treated herein probably are distantly related and do not represent a monophyletic group within the genus. The lustrous appearance of the vestiture shared by these species probably is a homoplastic feature within the genus. The shape of the aedeagus of *F. xanthuris* is highly unusual within *Filatima* and immediately separates it from the other species. Until a phylogenetic analysis is completed for all *Filatima*, a suitable hypothesis of relationships among species cannot be made.

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AN EXAMPLE OF CLINAL VARIATION IN EASTERN NORTH AMERICAN BUCKMOTHS (SATURNIIDAE: *HEMILEUCA*)

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ABSTRACT. Morphological variation in populations of eastern North American buckmoths was examined. Samples of 25 males each were analyzed from four points along a north-south line approximately 800 km long from Schoolcraft Co., Michigan to Vinton Co., Ohio. Clinal variation was demonstrated from higher to lower latitudes: (1) forewing length from smaller to larger; (2) forewing white band width from wider to narrower; and (3) darkness of the black background of the wing from lighter to darker. No logical way was found to separate these four populations into subspecies or species based on morphological characters.

Additional key words: *Hemileuca maia*, *H. nevadensis*, *H. lucina*.

The black and white buckmoths of the eastern United States and Canada have attracted much attention because of their showy wing patterns and unusual flight period very late in the season. Three species are usually attributed to eastern North America: in the western part *Hemileuca nevadensis* Stretch, in the northeast *H. lucina* Hy. Edw., and in the remainder of the area *H. maia* (Drury) (Ferguson 1971, Covell 1984). Each species is generally associated with a distinct food plant, all unrelated: willows (*Salix*: Salicaceae), meadowsweets (*Spiraea*: Rosaceae), and oaks (*Quercus*: Fagaceae), respectively.

We have surveyed various habitats and have verified, by egg mass placement and larval feeding, a more diverse range of food plants than is usually assumed (Scholtens & Wagner 1994). In addition, several populations are difficult to assign to any of the three recognized North American species. Some appear to be intermediate in maculation between *H. nevadensis* and *H. lucina* and others between *H. nevadensis* and *H. maia*. Here, using data on the characters typically used to distinguish the presently recognized species, we test the hypothesis that the populations in the Great Lakes region consist of a single species forming a cline ranging from relatively small, 'washed-out' looking forms in the north to larger, heavily marked forms in the south.

MATERIALS AND METHODS

We sampled and studied buckmoths at four localities in the Great Lakes region. From north to south these were: (1) Schoolcraft County in the Upper Peninsula of Michigan; (2) Roscommon County in the



FIG. 1. Map of sampling localities and example of male buckmoth from each.

central Lower Peninsula; (3) Washtenaw County in the southern Lower Peninsula; and (4) Vinton County in southern Ohio (Fig. 1). At each locality we made notes on the habitat and host plants used by the buckmoths and collected a series of 40–50 males, from which a sample of 25 in good condition were chosen for measurements and visual assessment. Vouchers from each population have been deposited at the University of Michigan Museum of Zoology.

A video image of each specimen was stored on a Macintosh II computer using the program NEH Image version 1.26. The lighting arrangement and the specimen-camera distance were not changed during image capture. For each image, measurements were taken, using Image, of forewing length from the base of the wing to the farthest point on the wing tip, and width of the white band on the forewing and hindwing along veins M_1 and CU_2 . The limits of the white band were easily determined by a sharp change over in scale color, even in the most diffusely

patterned moths. In addition, 10 pixel by 10 pixel areas were marked off on the forewing between veins CU_1 and CU_2 inside the white band and immediately distal to the white band. Using Image, an average darkness for each 100 pixel area was calculated based on a 256 point gray scale.

Because one characteristic difference between the populations was wing darkness, we did a microscopic examination of scale sizes and densities for the three Michigan populations, covering most of the variation in darkness. For 10 specimens from each population, we counted all scales in a 1.42×2.16 mm area of the forewing between veins M_3 and CU_1 , centered on the white band. In addition for 5 specimens from each population, 10 scales in one field of view were measured for length and width. For all data, comparisons among localities were made by ANOVA using the statistical package SYSTAT 5.0 for the Macintosh.

RESULTS

A great deal of variation exists in the habitats and host plants of Great Lakes buckmoths compared to previously published data. In the northern part of the range through southern Michigan, habitats are mainly wetlands, similar to those typically used by the western *H. nevadensis*, while in the south, upland wooded areas are prevalent. The host plants in wetland areas include willow, poplar, meadowsweet, and bog birch, and in the dry wooded sites, oaks (Scholtens & Wagner 1994).

Forewing length in the sampled populations varied from a mean of 24.04 mm in northern Schoolcraft County to 26.59 mm in southern Vinton County (Fig. 2). ANOVA shows that forewing length increases significantly from north to south ($F = 20.30$, $P = <0.001$). The width of the white band on the forewing decreases significantly from north to south (on M_1 : $F = 40.96$, $P = <0.001$; on CU_2 : $F = 24.47$, $P = <0.001$). On vein M_1 the mean width is 2.17 mm in Schoolcraft County and 0.61 mm in Vinton County. On vein CU_2 the mean width is 4.42 mm in Schoolcraft County and 2.60 mm in Vinton County (Fig. 3). Although the width of the white band on the hindwing varies significantly among the three populations (on M_1 : $F = 2.79$, $P = 0.045$; on CU_2 : $F = 15.30$, $P = <0.001$), we saw no demonstrable trend from north to south (Fig. 4).

There is a significant increase in the darkness of the white band from north to south ($F = 5.04$, $P = 0.003$), varying from Schoolcraft County with a mean of 82.97 gray scale units (out of 256) to Vinton County at 88.19 units. There is a much more pronounced significant increase in the darkness of the black areas of the wing from north to south ($F = 142.28$, $P < 0.001$), varying from 112.34 units in Schoolcraft County to 164.12 units in Vinton County (Fig. 5), with most of the change occurring from northern to southern Michigan. These means hide a great

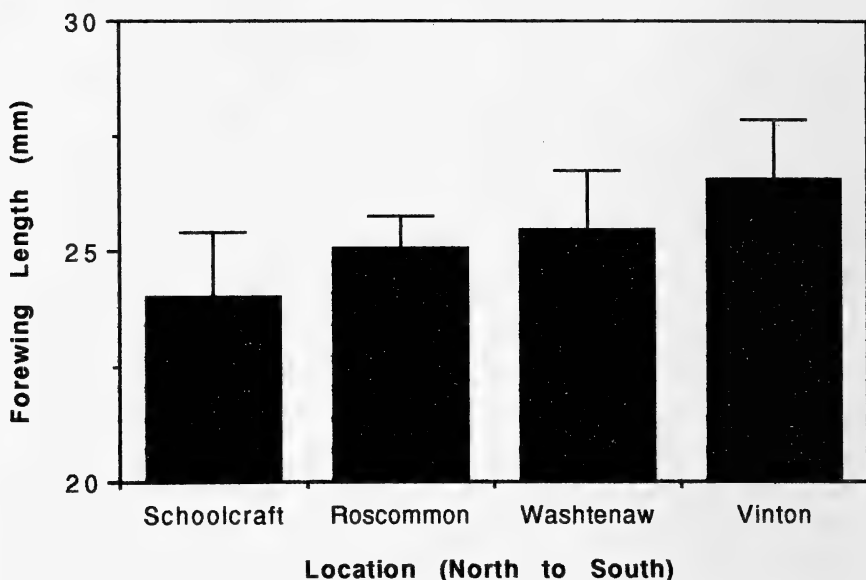


FIG. 2. Mean forewing length of sampled populations (error bars indicate standard deviation).

deal of variation in the darkness of the black areas of the wing, enough so that wing darkness overlaps in all adjacent populations (Fig. 6).

Darker wing color in the southern buckmoth populations is due to the size and distribution of wing scales. There are substantial differ-

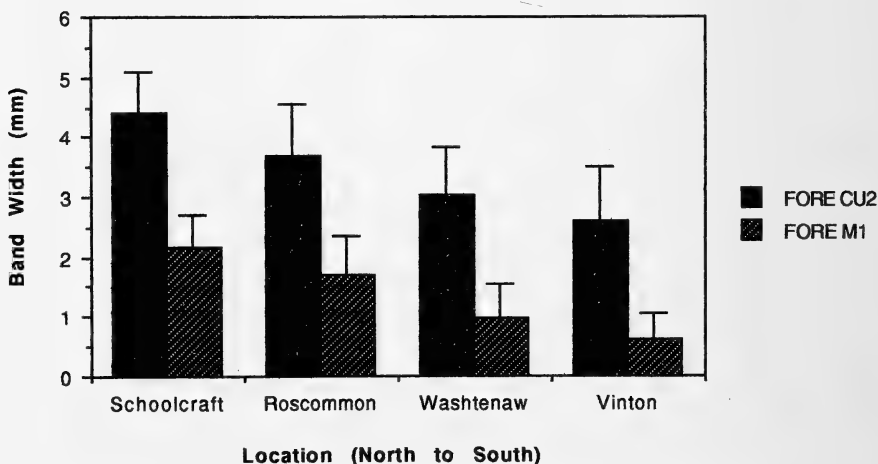


FIG. 3. Mean width of white band on forewing veins CU₂ and M₁ (error bars indicate standard deviation).

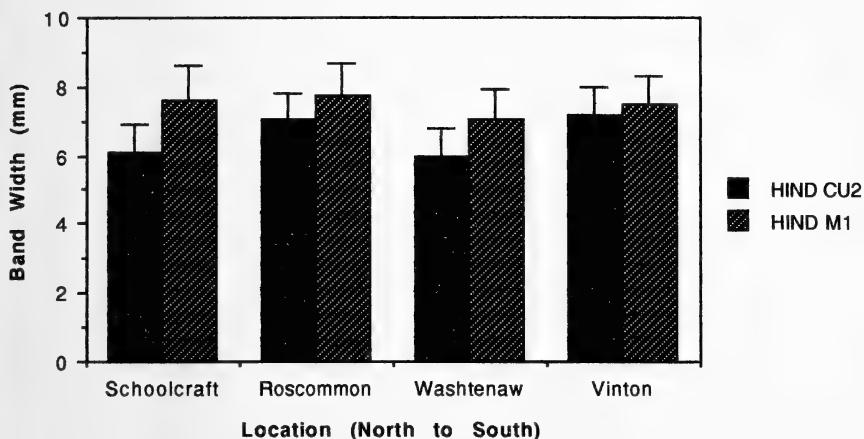


FIG. 4. Mean width of white band on hindwing veins CU_2 and M_1 (error bars indicate standard deviation).

ences in both size and density of scales among the populations (Figs. 7 and 8). From north to south, scale length ($F = 23.97$, $P = <0.001$), width ($F = 7.30$, $P = 0.008$) and density ($F = 26.97$, $P = <0.001$) increase significantly. All three of these parameters contribute to the lighter, more translucent appearance of the wings in the north.

Increasing forewing band width with decreasing wing length accentuates the trend of lighter colored wings in the north, and in Vinton County the ratio of band width to wing length is half or less of that in

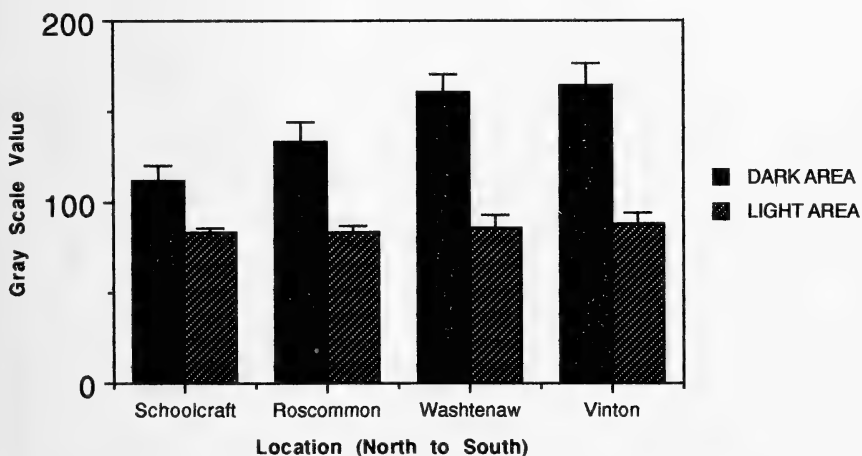


FIG. 5. Mean darkness of light and dark areas of forewing (error bars indicate standard deviation).

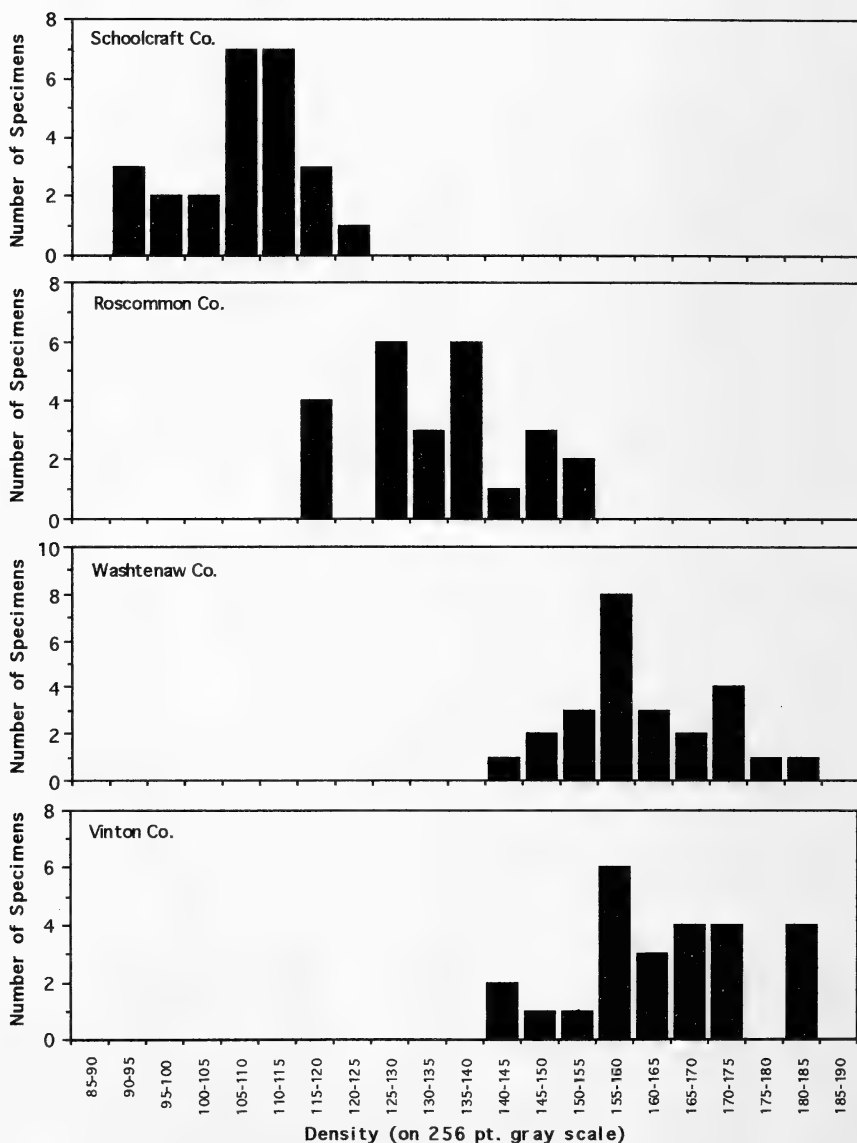


FIG. 6. Distribution of wing darkness at the four study sites.

Schoolcraft County. Also influencing this impression is a proportionally greater increase in width at the center of the white band as you proceed north. The ratio of the width of the white band on vein M_1 to the width on vein CU_2 decreases to less than half of the Schoolcraft County value in Vinton County.

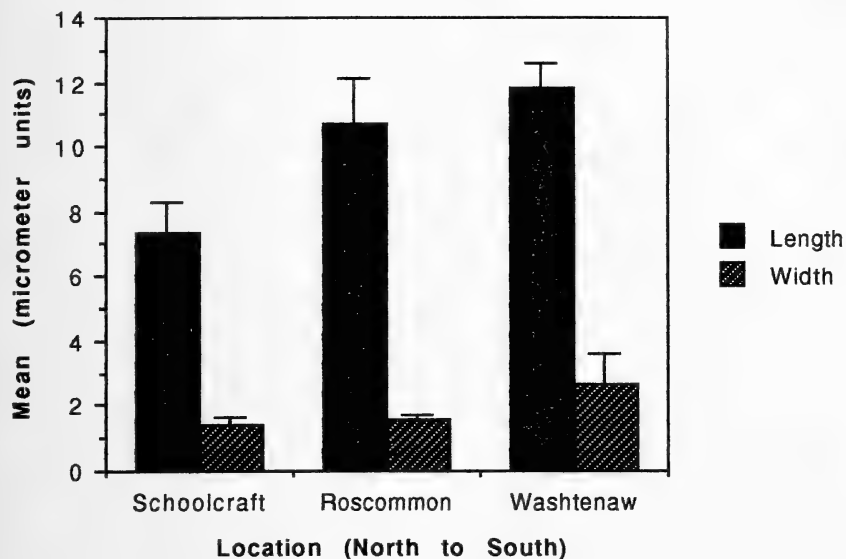


FIG. 7. Mean scale length and width (error bars indicate standard deviation).

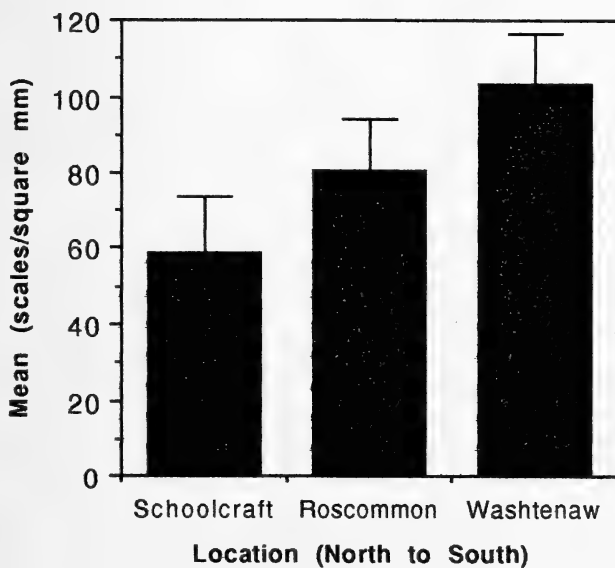


FIG. 8. Mean scale density (error bars indicate standard deviation).

DISCUSSION

Our results clearly demonstrate correlated changes in food plants and maculation characters of buckmoths along a north-south line in the Great Lakes region. Where the wing length is smaller in the north, the white band is wider and the black background is paler. The northernmost element is most similar to the New England buckmoth, *Hemileuca lucina*, the southernmost element is most similar to *H. maia*, and the intermediates resemble some of the forms of the widespread western buckmoth, *H. nevadensis*. There is also a general correlation with habitat, bogs and fens in the north and upland, oak woods in the south. The larval food plants include bog birch (*Betula pumila* L.: Betulaceae), willows (*Salix* spp.) and meadowsweets (*Spiraea* spp.) northward and oaks (*Quercus* spp.) in the south (Scholtens & Wagner 1994).

Change in maculation of buckmoths is a direct result of a change in scale size and density. Scale density in the northern populations decreases, even when corrected for the reduction in wing size, and scale size also decreases proportionally much more than wing size. The existence of a north-south morphological cline in *Hemileuca* should not be surprising. Good examples of latitudinal clines exist in other widespread species in North America (e.g., *Cercyonis*, Emmel 1969), Great Britain (e.g., *Coenonympha*, Porter 1980), and Australia (e.g., *Tisiphone*, Lucas 1969). In our experience, forms of non-migratory species in the extreme north tend, in general, to be smaller and the pattern less contrasting than those from the south. The same is often true of spring versus summer forms.

Some speculations about possible evolutionary causes of size and maculation changes in northern populations are the following: (1) smaller size may simply be a result of a shorter growing season; and (2) scale development may be aborted because of the shorter pupal period in northern populations (late June through late August in the north versus mid-June through early October in the south). These remain speculations until experimental work can verify or refute them.

Confusion about the nomenclature of *Hemileuca* populations has existed for many years as evidenced by the naming of *H. latifascia* Barnes and McDunnough as a subspecies of *H. lucina*, followed by its synonymization with *H. nevadensis* (Ferguson 1971). Forbes (1960) even remarked on the intermediacy of *H. latifascia* between *H. maia* and *H. lucina*. Great Lakes populations have always been vexing because willow feeders have periodically been reported from the region (Ely 1954, Riley 1873, Worthington 1878), but not studied carefully. Our data show that no good maculation differences exist that allow Great Lakes populations to be placed confidently into one of the recognized species. Likewise, the host

plants and habitats are not distinctive and do not serve to identify populations definitively as once thought. Ferge (1981) documented similar within population variation in Wisconsin, and populations in Minnesota, and the eastern United States also resemble those we studied. Legge et al. (1996), in a study examining allozyme differences in *Hemileuca* populations from across the country, found very few differences between any of the populations examined, and suggested that these populations could still be considered distinct species based on ecological differences. Our data would not support this, showing that ecological differences among the various populations are not consistent (Scholtens & Wagner 1994). Although separate eastern populations may seem quite distinct, local population differentiation may be more prevalent in this region because of longer isolation due to habitat fragmentation.

The patterns seen in this study could result from variation within a single species or from a hybrid zone between distinct species. Our data cannot distinguish between these alternatives, but the most satisfying explanation for our findings is that all populations represent a single species showing clinal variation from north to south. A species distinction could exist between the wetland populations that feed on birch, poplar, meadowsweet and willow and the upland, oak-feeding populations. Ecologically, these appear distinct and some evidence indicates that they may be isolated by pheromone differences (James Tuttle, pers. comm.), but these differences are not indicated by the clinal nature of the morphological variation. If all populations are a single species they would be referred to as *H. maia* (Drury). If two entities exist, the upland populations would be *H. maia* (Drury) and the wetland ones *H. nevadensis* Stretch. This question may be decided conclusively by careful hybridization and rearing studies between geographically close populations of both types.

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A NEW SPECIES OF RIODINIDAE FROM COLOMBIA

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ABSTRACT. A new riodinid species, *Calydna volcanicus*, from Cerro Aguacatal and Cerro Clavijo in the western department of Caldas, Colombia, is described and illustrated. Comments on its habitat and adult behavior are presented, with a list of other Riodinidae found in the same habitat and a range extension for *Amphiselenis chama* (Staudinger 1888).

Additional key words: neotropical South America, coffee plantations.

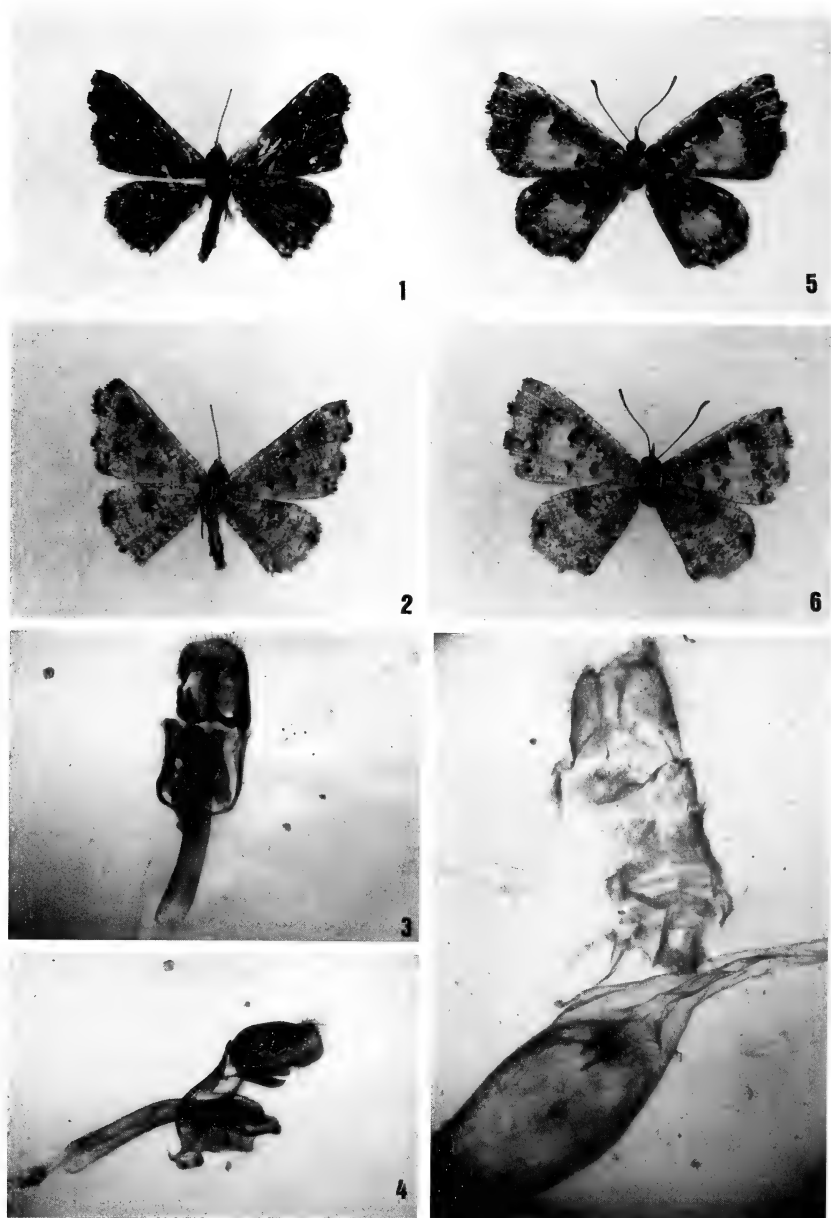
Forests at altitudes between 1300 and 2200 m in the Colombian Andes are fertile for the discovery of new and interesting riodinid butterflies (Callaghan 1983, Salazar & Constantino 1993, Salazar, 1993). An unusual habitat for riodinids described in this paper consists of coffee plantations, considered to be an example of extreme habitat alteration. In these situations, the original forest has been completely destroyed except for some of the taller trees that have been left to shade the coffee. If insecticides have not been used extensively, this altered habitat can support a diverse fauna.

The purpose of this paper is to describe a new species of *Calydna*, and present comments on the coffee zone habitat and some of the other riodinid species found there. The description is based on material collected by J. Escobar at the localities noted below. Measurements were done with a caliper, and the genitalia were prepared by soaking in 10% KOH solution and examined under a binocular microscope. Terminology for the genitalia follows Klots (1970) and that for veins and cells follows the Comstock-Needham system (Miller 1969). The citing of Riodinidae as a family instead of a subfamily follows Harvey (1987).

Calydna volcanicus Callaghan & Salazar, new species (Figs. 1-7)

Description. Eyes brown, not hairy, surrounded by white scaling; palpi dimorphic, those of female longer than male; antenna length 6.4 mm, 0.59 length of forewing; shaft with white scales between segments, club flat, spoon shaped; forewing costa straight, apex pointed, distal margin scalloped at the end of cell M_3 -CU₁; hindwing with apex rounded, margin scalloped between CU2 and 2A; anal angle pointed, inner margin straight; fringe light brown.

Male (Figs. 1, 2): forewing length of holotype 13 mm, range of material examined 11-13 mm (n = 3). Thorax ventrad and appendages with long, white hairs; abdomen brown with



FIGS. 1-7. *Calydna volcanicus*, new species. 1, male holotype, dorsal surface; 2, same, ventral surface; 3, male genitalia, caudal view; 4, same, lateral view; 5, female, dorsal surface; 6, same, ventral surface; 7, female genitalia.

long, white hairs ventrad on first 5 segments; long, lateral scent hairs on last segment. Dorsal surface of wings dark brown with faint black and orange maculations and black distal margins. Forewing with two faint black parallel lines at end of cell, a single spot below the cell between CU_2 and 2A and faint disperse orange scaling in discal area between CU_2 and 2A. Hindwing with 2 faint parallel black lines beyond end of cell and long disperse scent hairs in discal area. Ventral surface light brown with striated dark brown maculations. Forewing with two large black spots beyond end of cell; one in cell CU_1 and three in cell CU_2 . Hindwing with numerous black maculations. *Genitalia* (Figs. 3, 4): with socii unlobed; gnathos simple, unmodified; vinculum narrow, slightly bowed halfway down each side, saccus small, pointed; valvae broad with two protrusions, dorsad and basad, the dorsal protrusion longer and curving inward; transtilla broad, rounded caudad; annellus with a long, pointed process curving caudad; aedeagus with the tip forming a broad plate with teeth projecting caudad.

Female (Figs. 5, 6): forewing length 13.0–13.5 mm ($n = 2$). Body dark brown dorsad, white ventrad. Dorsal surface of wings dark brown and yellow-orange with black maculations. Forewing with discal area between M_3 and 2A orange-yellow, extending to M_1 past end of cell, and with some scattered orange-yellow scaling within cell; two black spots in cell M_1 beyond cell and two in cell CU_2 below discal cell. Hindwing with large irregular yellow-orange spot in discal area between R_s and cell 2A; limbal area with faint, irregular dark brown spots along margin between the veins. Ventral surface light brown and light orange, with lighter brown maculations. Forewing submargin white with brown maculations; discal area with light yellow spot as in dorsal surface; three black spots in discal cell, one in cell CU_1 and three in cell CU_2 . Hindwing distal half white with numerous dark brown striated maculations; basal half same but with ground color light brown. *Genitalia* (Fig. 7): with ostium bursae opening wide with sclerotized process cephalad; ductus seminalis joins ostium bursae at same point as ductus bursae; corpus bursae with two blunt siga; located far cephalad in abdomen, concurrent with segments A2–A4; papillae anales rounded, setose.

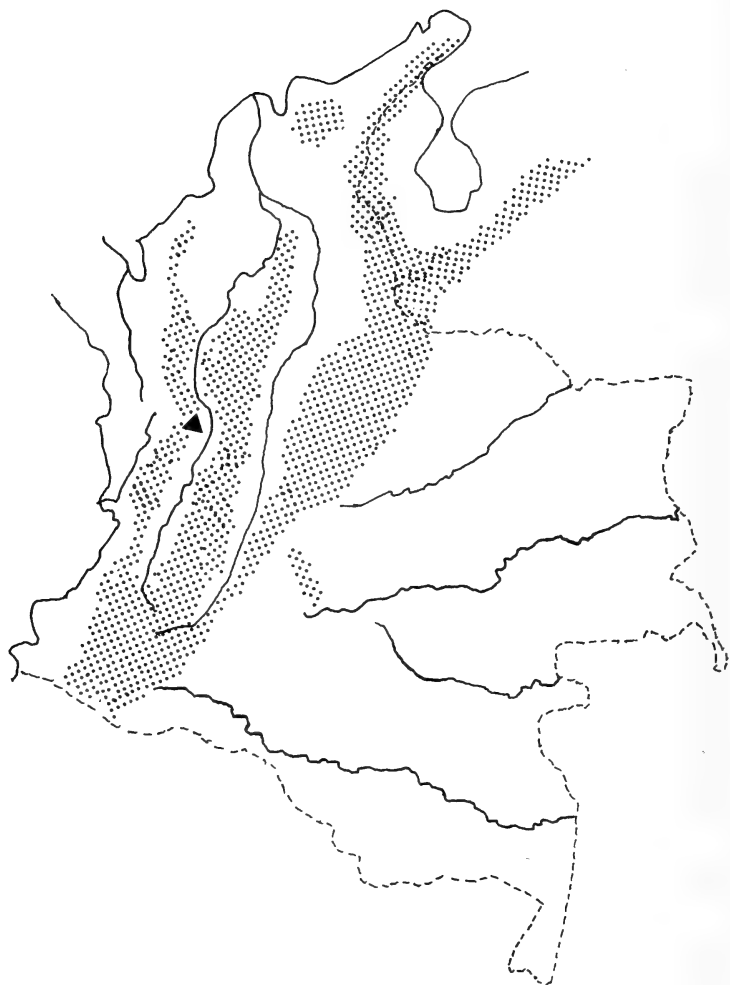
Types. *Holotype*: male, Cerro Aguacatal, Mpio Riosucio, Caldas, Colombia, 15 April 1993, leg. Salazar. *Paratypes*: 6 males, 2 females as follows: Cerro Aguacatal, Mpio Riosucio, Caldas 1300 m, 1 April 1994; Cerro Clavijo, Mpio Riosucio, 20 July 1994. The holotype is deposited in the Museo de la Universidad Nacional, Bogota, Colombia. The paratypes are in the collections of C. Callaghan, J. LeCrom, and E. Schmidt-Mumm of Bogota, and the Universidad de Caldas, Manizales.

Diagnosis. *Calydna volcanicus* is closely allied to *Calydna hemis* Schaus from southeastern Brazil, and therefore is provisionally assigned to the same genus. However, both these species differ from *Calydna thersander* (Stoll), the type species of the genus, in the large, sexually dimorphic palpi and the structure of the genitalia, suggesting that they belong to an undescribed genus.

Distribution and Habits. The species was discovered by J. Escobar on two small mountain ranges, Cerro Aguacatal and Cerro Clavijo, both on the eastern slope of the Cordillera Occidental in the Municipio of Riosucio, Caldas Department between 1200 and 1600 m above sealevel (Fig. 8). The climate is Very Humid Premontane Forest (IGAC 1977) with a mean annual rainfall of 2000–4000 mm and a biotemperature of between 18–24°C. The area has been extensively cultivated for coffee (*Coffea arabica*) with the consequent alteration of the original vegetation. The upper slopes of the Cerro Aguacatal (1300 m) are practically devoid of vegetation and a concrete cross is at the summit. *Calydna volcanicus* flies below the summit in a deep canyon with low bushes growing on the slopes. Males perch on low bushes after 1200 h, resting with wings spread on the upper leaf surface. When disturbed, they fly rapidly, engaging other males in a whirling chase before returning to their original spot. The lower slopes of the Cerro Aguacatal (1500–1600 m) and the Cerro Clavijo are occupied with coffee plantations shaded by native trees of the genera *Inga* and *Albizia*. Here, males perch along trails through the plantations between 1300–1400 h, always on the upper leaf surfaces with wings spread. Females frequent the same areas and visit flowers.

Etymology. The name *volcanicus* has no significance.

Other riodinid species recorded from the same habitat include: *Siseme pallas*



8

FIG. 8. Map of Colombia. Hatched areas represent zones above 1000 m. Triangle indicates type locality of *Calydna volcanicus*.

(Latreille), *Catocyclotis elpinice* (Godman), *Amphiselenis chama* (Staudinger), *Melanis cratia* (Hewitson), *Adelotypa densemaculata* (Hewitson), *Charis* nr. *zama* (Bates), and *Calephelis schausi* McAlpine. The discovery of *Amphiselenis chama* in north central Colombia constitutes an extension of its previously known range in the Venezuelan Andes. Examination of *Amphiselenis* from both Colombia and Venezuela revealed no consistent variation in phenotype between the two populations.

ACKNOWLEDGMENTS

We thank Luis Constantino and an anonymous reviewer for their helpful comments.

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A REVISION OF THE *EUSELASIA ORFITA* COMPLEX (RIODINIDAE)

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ABSTRACT. The *Euselasia orfita* complex (Riodinidae) *sensu* Stichel 1919 is revised. Separate keys to adult males and females are presented, as well as notes on nomenclature, geographical variation, distribution and adult habits. As revised, this complex includes: *E. orfita* (Cramer 1777); *E. eutyclus* (Hewitson 1856) **reinstated status**, =*E. ferrugo* (Bates 1868) **new synonym**; *E. cuprea* Lathy 1926 **reinstated status**; *E. cyanira* **new species**; *E. clithra* (Bates 1868), =*E. clithra jugata* Stichel 1919 **new synonym**; and *E. phedica* (Boisduval 1836).

Additional key words: neotropical, South America, Brazil, Colombia, Peru, Ecuador.

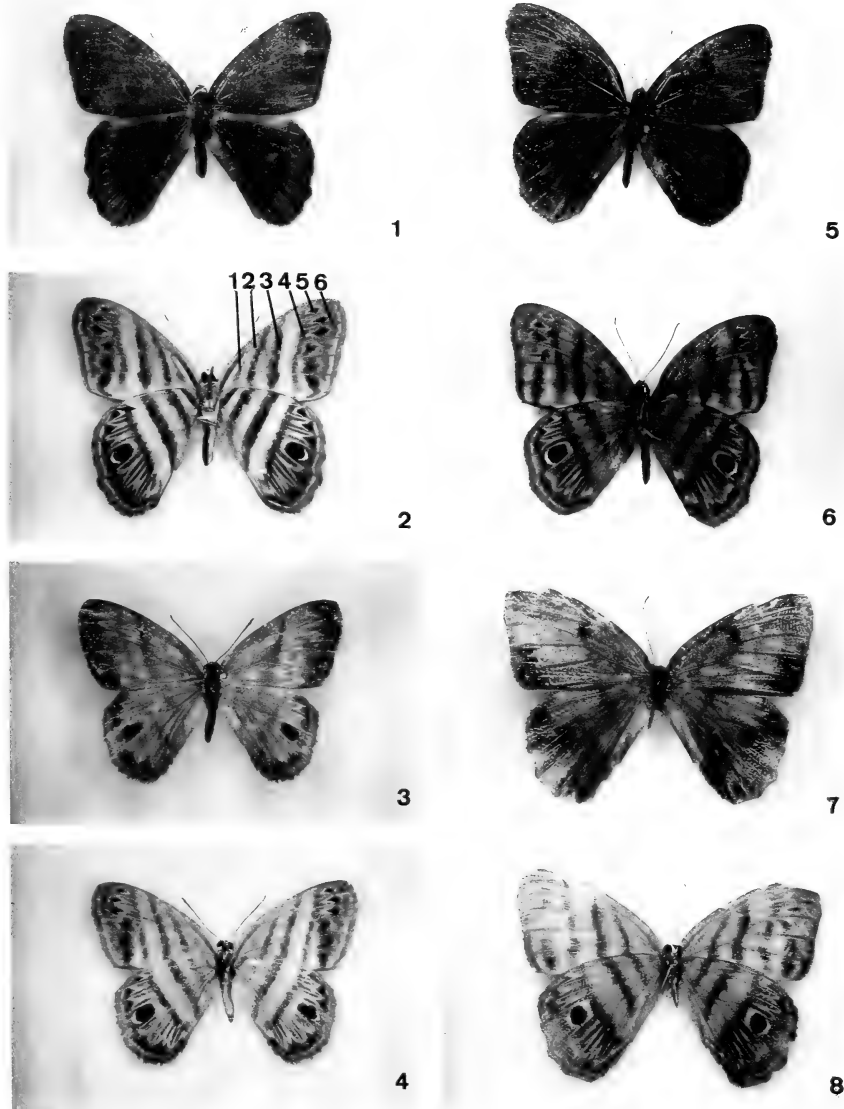
The purpose of this paper is to revise the *Euselasia orfita* complex (Riodinidae), a small assemblage of species inhabiting South America east of the Andes. Although common in museum collections, these species are difficult to identify because they are similar in appearance, especially females. This revision is preliminary because other *Euselasia* species may belong to the *E. orfita* group. For this reason, a phylogeny will be attempted only later, when confidence about the systematics of this large and varied genus is on a firmer foundation.

MATERIALS AND METHODS

In addition to the author's collection (CJC), the following institutional collections were consulted during this study: Museu Nacional, Rio de Janeiro (MN); Smithsonian Institution, Washington D.C. (NMNH); Muséum National d'Histoire Naturelle, Paris (MNHN). A total of 256 specimens was examined, including 36 specimens taken on loan. Thirty eight genitalic preparations were made by soaking the abdomens overnight in 10% potassium hydroxide solution; genitalia were stored in vials cross referenced to the specimens. Terminology of the genitalic structures follows Klots (1970), and the designation of wing veins and cells follows Miller (1969). Measurements were made using a binocular microscope fitted with an ocular micrometer. Field observations were made by CJC unless otherwise indicated.

MORPHOLOGY OF THE *EUSELASIA ORFITA* COMPLEX

The species of the *E. orfita* complex are easily separated from other *Euselasia* by their large size (forewing length 17–24 mm), and the series of parallel dark red/brown bands that cross the ventral surface of both wings. Other distinguishing characteristics of the complex are as follows:



FIGS. 1–8. Adults of *Euselasia orfita* complex. 1, *E. orfita*, dorsal, male (Brazil); 2, ventral, male, showing numbering of bands; 3, dorsal, female (Brazil); 4, ventral, female; 5, *E. cuprea*, dorsal, male; 6, ventral, male; 7, dorsal, female; 8, ventral, female;

Dorsal wing pattern. The male dorsal wing pattern characterizing the *E. orfita* group can best be seen using light projecting from behind the viewer's shoulder, with specimens tilted away from the viewer from the apex towards the base of the wings. There are three distinct arrangements of iridescent blue scaling on the forewing. In the first, the color is deep purple and confined to the basal half (Fig. 1). In the second, the color is lighter blue

and the pattern consists of a wide >3 mm band beginning at the costa above the cell, that curves around the end of the cell and terminates at the inner margin, and with darker blue-violet between the band and the base; the distal area lacks iridescent scaling (Fig. 9). In the third, there is a thin band 1 mm wide beginning at the base that continues along the margin to distad of the cell, and then crosses the wing as a 2 mm wide band to the inner margin, with dark blue scaling on both forewing and hindwing separated from the thin band by a black area (Fig. 21).

The pattern on the hindwing likewise consists of three types: a deep purple tone in the distal half (Fig. 1); a marginal band of light blue scales (Fig. 9); or a white limbal area with a glossy light blue sheen (Fig. 25).

Ventral wing pattern. The *E. orfita* group is characterized by a ventral forewing pattern that includes six bands crossing the forewing from the costal margin to 2A, and the hindwing from the costa to the inner margin. These are numbered 1–6 from the base to the submargin in Fig. 2. Bands 1–4 are reddish brown and band 1 is thinner and shorter. The first three bands are slightly convergent toward the forewing costa. Band 5 is broken into a series of figures consisting of spots and lines, and band 6 follows the margin of both wings as a distinct band or shading. The bands are the principal means of associating the sexes.

On the forewing, the shape of band 4 may be straight (Fig. 10) or S-shaped (Fig. 6) in both sexes. Band 5 begins as three arrow-shaped spots in cells R_3 – R_4 , R_4 – M_1 , and M_1 – M_2 , followed by a wide band between M_3 and 2A on the inner margin. The band between M_3 and 2A has three types: a straight heavy line to 2A, veering basad to the inner margin as a thin projection (Fig. 2); a band curved towards the costa, uniting with band 4 at M_3 (Fig. 6); straight as above, but not reaching below 2A (Fig. 10).

The ventral hindwing is characterized by the continuation of bands 1–4 from the forewing. Band 5 becomes a series of arrowhead-shaped spots pointing basad between the veins, with a blue ocellus in cell M_2 – M_3 , bordered on three sides with orange and distad by white. The distance between the ocellus of the hindwing ventral surface and band 3 differs significantly between species, and is greater in females.

Genitalia. The male genitalia (Figs. 29–34) are simple with a broad bilobed uncus widely separated from the tegumen, the latter with two narrow falces and joined to the valvae by a long, thin vinculum. The saccus consists of a widening of the base of the vinculum. The valvae are elongate, spatula-shaped with flat tips and a heavily sclerotized process near the base. The aedeagus is blunt or pointed, with a coiled vesica and is guided by a sclerotized triangular-shaped transtilla. There is considerable intraspecific variation.

In the female genitalia (Figs. 35–39) the lamella postvaginalis is bladelike with a small point between the two blades. The posterior ductus bursae has two tiny crescent-shaped signa. There appeared to be considerable differences among the genitalia examined; however, the number of preparations was insufficient to separate specific from individual variation with confidence.

Frons and palpi. The lateral margins of the frons and palpi are either dirty yellow or white.

Geographic distribution. The *E. orfita* complex is limited to tropical South America east of the Andes from the Guianas across the Amazon basin to Peru (Bolivia?). In the Andes the complex occurs up to 1000 m (Fig. 40).

PROPOSED CLASSIFICATION

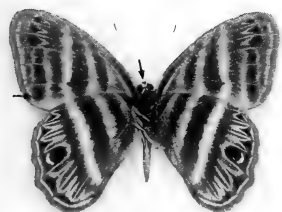
In his revision of *Euselasia*, Stichel (1928) recognized nine species in this complex (Orfitoformes): *E. orfita* (Cramer), *E. ferrugo* (Bates), *E. clithra* (Bates), *E. phedica* (Boisduval), *E. eurymachus* (Hewitson), *E. eurysthenes* (Hewitson), *E. orba* Stichel, *E. issoria* (Hewitson) and *E. euodia* (Hewitson). Examination of the latter five species suggests that they are not related to the *Euselasia orfita* complex. They lack the six band pattern on the wing ventral surface typical of *E. orfita*. On



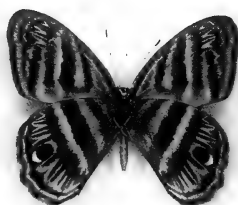
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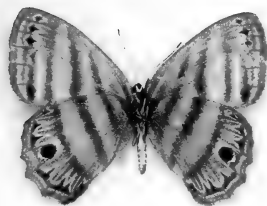
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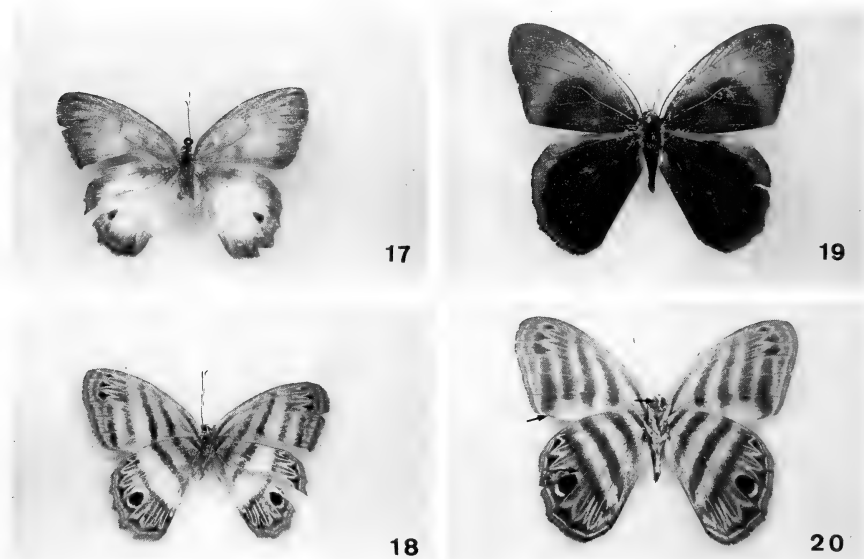
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FIGS. 9–16. Adults of *Euselasia orfita* complex. 9, *E. eutychus*, dorsal, male (Brazil, AM); 10, ventral, male; 11, dorsal, female (Brazil, AM); 12, ventral, female; 13, dorsal, male (Brazil, PA); 14, ventral, male; 15, dorsal, female (Brazil, PA); 16, ventral, female.

E. eurymachus and *E. eurysthenes* the tips of the valvae are bifurcated with the lower projection longer and turned inwards, a characteristic of the *Euselasia anica* complex (*Aniciformes sensu* Stichel). Although the male genitalia of *E. orba*, *E. euodia* and *E. issoria* are close to *E. orfita*,



FIGS. 17–20. Adults of *Euselasia orfita* complex. **17**, *E. eutyclus*, female (Brazil, PA); **18**, ventral, female; **19**, *E. cyanira*, holotype, dorsal; **20**, ventral.

the wing pattern suggests that they form a distinct monophyletic group. Thus, all five taxa are omitted from consideration in this paper. The following classification for the *E. orfita* complex is proposed:

E. orfita (Cramer 1777)

=*E. orfita eutyclus* f. *truculenta* Stichel 1924

E. eutyclus (Hewitson 1856), **reinstated status**

=*E. ferrugo* (Bates 1868), **new synonym**

=*E. dyrrhachius* Seitz 1913

=*E. eutyclus* f. *lacteata* Stichel 1919

=*E. orba spectralis* f. *pallida* Lathy 1926

E. cyanira, **new species**

E. cuprea Lathy 1926, **reinstated status**

E. clithra (Bates 1868)

=*E. jugata* Stichel 1919, **new synonym**

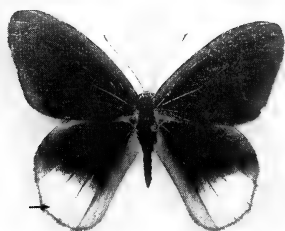
E. phedica (Boisduval 1836)

KEY TO MALES OF THE *E. ORFITA* COMPLEX

- | | |
|---|---|
| 1a. Dorsal forewing with a blue band across forewing from end of cell to inner margin. | 4 |
| 1b. Dorsal forewing dark purple with no transverse band. | 2 |
| 2a. On ventral surface of forewing, space between lines three and four lighter than | |



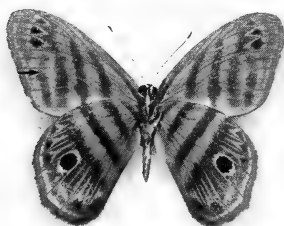
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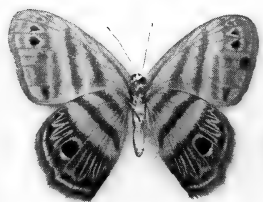
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FIGS. 21-28. Adults of *Euselasia orfita* complex. 21, *E. clithra*, dorsal, male (Brazil, PA); 22, ventral, male; 23, dorsal, female (Brazil, PA); 24, ventral, female; 25, *E. phedica*, male (Fr. Guiana); 26, ventral, male; 27, dorsal, female (Fr. Guiana); 28, ventral, female.

ground color; line four straight, line five to CU_2 ; distance between ocellus and third band 0.8-1.0 mm; valvae short, flat, tips rounded. *E. orfita*
 2b. On ventral surface of forewing, ground color uniform; line four S-shaped; line five curved from $2A$ to M_3 ; line five to M_3 3

- 3a. Hindwing dorsal surface black with dark blue margin; ocellus distance 0.7–1.0 mm; valvae wide, tips flat, spatula-shaped. *E. cuprea*
- 3b. Hindwing dorsal surface with white limbal area; line three on ventral forewing S-shaped; line four curved and yellow; line five reaches M_3 ; ocellus distance 0.3–0.8 mm; valvae very short, slightly flattened. *E. phedica*
- 4a. Forewing with wide >3 mm blue band crossing discal area to inner margin 5
- 4b. Forewing with thin <3 mm blue band from base to end of cell, then crossing wing to tornus; ventral forewing line five wide to 2A, then turning basad as a thin line to inner margin; populations in eastern Amazon basin with bands three and four more widely separated with white scaling; ocellus distance 0.8–1.8 mm; valvae long, round, slightly curved inwards, tips rounded. . . . *E. clithra*
- 5a. Facial sutures white; dorsal wing surface with ventral surface markings showing through; ventral surface covered uniformly with a blue glaze; line four reaching beyond 2A as thin line turning basad to inner margin; ocellus distance 0.7–1.1 mm; valvae like *E. clithra*, slightly longer *E. cyanira*
- 5b. Facial sutures yellow; dorsal wing surface opaque; ventral surface blue glaze confined to base of forewing and anal angle of hindwing; line four stopping at 2A; ocellus distance 0.5–0.9 mm; valvae very long, narrow, tips pointed and turned inwards *E. eutyclus*

KEY TO FEMALES OF THE *E. ORFITA* COMPLEX

- 1a. Ventral forewing lines four and five curved costad, meeting at M_3 2
- 1b. Ventral forewing lines four and five straight. 3
- 2a. Ventral hindwing ocellus in cell M_2 – M_3 round, less than 0.9 mm from band four; band four on forewing yellow; dorsal grey-blue; ocellus distance 0.96 mm *E. phedica*
- 2b. Ventral hindwing ocellus in cell M_2 – M_3 <1.1 mm from band three; band four on forewing reddish brown; dorsal brown; ocellus distance 1.1 mm *E. cuprea*
- 3a. Palpi, facial sutures yellow; ocellus on ventral hindwing <1 mm from band four; dorsal hindwing ocellus arrowhead-shaped; individuals may have white discal area ventrad or dorsad; ocellus distance 0.7–1.0 mm *E. eutyclus*
- 3b. Palpi, facial sutures white; ocellus on ventral hindwing <1 mm from band four 4
- 4a. Dorsal hindwing with yellow scaling around ocellus; ventrally with ground color between bands three and four slightly lighter; forewing lines five and six wide, broken, indistinct; ocellus distance 1.2–1.4 mm *E. orfita*
- 4b. Dorsal hindwing without yellow scaling; ventral forewing bands five and six narrow, of uniform width, unbroken; ground color uniform; ocellus distance 1.6–2.1 mm *E. clithra*

SPECIES ACCOUNTS

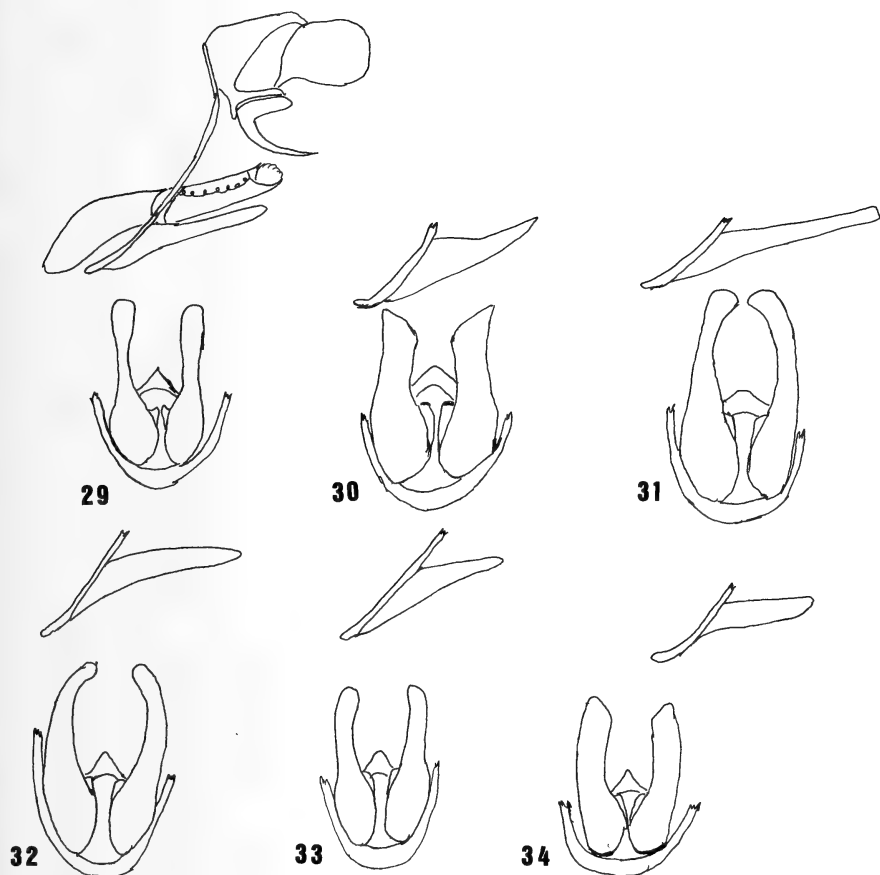
Euselasia orfita (Cramer 1777)

(Figs. 1–4, 29, 35)

Nomenclature. Cramer (1777) described *Euselasia orfita* from a male from Surinam. Figures D and E on his plate 112 are crude, but recognizable as *E. orfita*. The type apparently has been lost, and there is no specimen at Leiden that could be designated as a lectotype. However, the species is distinct.

Geographical Variation. The species shows little variation over its range from the Guianas to Brazil (Para, Amazonas). A single female from “Santa Cruz Bolivia” at the MNHN is probably mislabeled.

Ecology and Behavior. *Euselasia orfita* inhabits terra firme forests in the lowlands of the Amazon basin and the Guianas. Males are encountered rarely in the forests perching in the early afternoon in treefalls and other small clearings, resting under leaves near the ground with their wings closed. When searching for oviposition sites, female *E. orfita* often rest on the upper surfaces of leaves, and this habit, along with the barred wing undersides and loping flight, make it easy to confuse them with satyrids.



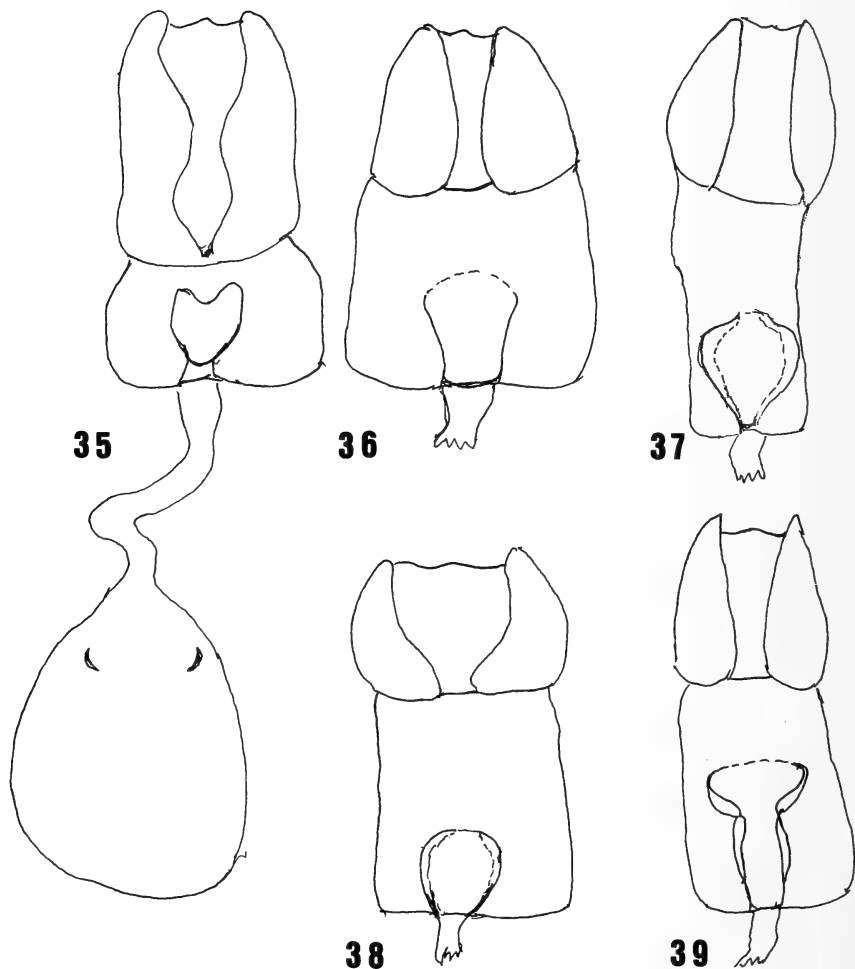
FIGS. 29–34. Male genitalia of *Euselasia orfita* complex. 29, *E. orfita*; 30, *E. cuprea*; 31, *E. eutychnus*; 32, *E. cyanira*; 33, *E. clithra*; 34, *E. phedica*.

Material Examined. FRENCH GUIANA: St. Elie pk 15.5 on D21, 7♂ (NMNH); Moyen Maroni, 1♂ (MNHN); Kana (Mana?), 1♂ (CJC); St. Laurent, 4♂ 1♀ (MNHN). BRAZIL: Obidos, Pa, 1♂ (NMNH), 3♂ (MNHN); Trombetas, Pa., 1♂ (MNHN); Tapajós, Pa, 1♂ (MNHN); Manaus, Am, 1♀ (MNHN); Tefé, Am, 1♀ (MNHN); 80 km N. Manaus, Am, 7♂ 4♀ (CJC). BOLIVIA: Santa Cruz, 1♀ (MNHN)(?).

Euselasia cuprea Lathy 1926, **reinstated status**
(Figs. 5–8, 30, 36)

Nomenclature. This species was described from a male, currently in the British Museum (Natural History). The type locality is St. Laurent, Maroni River, French Guiana. Stichel (1928) treated *E. cuprea* a subspecies of *E. orfita*. However, the two are distinct morphologically, and sympatric.

Geographical Variation. The species is confined to the Guianas and shows no variation among the material examined.



FIGS. 35-39. Female genitalia of *Euselasia orfita* complex. 35, *E. orfita*; 36, *E. cuprea*; 37, *E. eutyclus*; 38, *E. clithra*; 39, *E. phedica*.

Ecology and Behavior: The species inhabits the terra firme forests of French Guiana. I have no personal experience with its habits.

Material Examined. FRENCH GUIANA: Rte. de l'Est, 1♂ (NMNH); St. Jean Maroni, 1♂ (NMNH); PK43.5 N2, 3♂ (CJC); Nouveau Chantier, 2♂ 2♀ (MNHN); "Guyane Française," 2♂ (MNHN); T. Laurent, 1♀ (MNHN); St. Domenti, 1♂ (CJC); Galion, 1♂ (CJC).

Euselasia eutyclus (Hewitson 1856), **reinstated status**
(Figs. 9-18, 31, 37)

=*Euselasia eutyclus* f. *pallida* Lathy 1926

=*Eurygona ferrugo* (Bates 1868)



FIG. 40. Geographical distribution of the *Euselasia orfita* complex. Filled circles = *E. orfita*, filled triangles = *E. eutyclus*, filled squares = *E. phedica*, open circles = *E. clithra*, open triangles = *E. cyanira*, open squares = *E. cuprea*.

=*Euselasia dyrrachius* Seitz 1913

=*Euselasia orba spectralis* f. *lacteata* Stichel 1919

Nomenclature. Hewitson (1856) described *E. eutyclus* from a male, presently in the British Museum (Natural History), with the label indicating "Amazon" as the locality. His figures 44 and 46 are good representations of the species. Stichel (1919) placed *E. eutyclus* as a subspecies of *E. orfita* with no explanation. As in the case of *E. cuprea*, this was in error, as the two are distinct morphologically, as well as partially sympatric.

Geographical Variation. There is significant variation both within and between populations of *E. eutyclus* from Pará and Amazonas, Brazil, south of the Amazon River, to the foothills of the Andes from Meta, Colombia, south to Peru. In males from Pará, band 5 converges sharply from the anal angle towards band 4; in males from Amazonas, Brazil, Peru and Colombia this band is parallel to band 4. In some males, bands 3 and 4 fuse

together (*ferrugo* Bates). Females show variability paralleling that of the males. Those from Pará are generally darker than those to the east and have wider bands. Some individuals have white ventral hindwing surfaces, and others have white on the discal area of the dorsal surface (*pallida* Lathy, and *lacteata* Stichel; Figs. 17–18). The white scaling is variable and is rare although present in all *E. eutychnus* populations.

Ecology and Behavior. *Euselasia eutychnus* is widespread, from Pará, Brazil, throughout the Amazon Basin to Peru. Unlike other members of the group, it adapts to disturbed habitats where it may be locally common. I have found the males perching in the late morning inside the edges of large clearings, resting on ventral leaf surfaces with their wings folded. Females are found less commonly within the forests.

Material Examined. BRAZIL: Jaru, RO, 3♂ (CJC); Cuiabá-Santarem km 1666, Pa, 4♂ (CJC), 1♂ 1♀ (NMNH); Vila Bela, MT, 1♂ (CJC); Vilhena, RO km23, 2♂ (CJC); Manaus, AM, 1♂ (CJC); Trombetas, Pa, 2♂ 1♀ (MNHN); Faro, Pa, 2♂ 1♀ (MNHN); Maués, Am, 1♂ (MNHN); Tefé, Am, 1♂ (MNHN); Conceição, Tapajós, Pa, 3♂ (MNHN); Santarém, Pa, 4♂ (MNHN); Tapajós, Pa, 2♂ (MNHN); Itaituba, Pa, 1♂ (MNHN); Amazon Sup., 2♂ 1♀ (MNHN); Vista Alegre, Rio Jurua Mirim, Acre, 1♂ (KB). COLOMBIA: Puerto Inirida, Putumayo, 1♂ (CJC); La Macarena, Meta, 1♂ (CJC); Letícia, Am, 2♂ (CJC); Villagarzon, Caquetá, 3♂; Rio Negro, Meta, 5♂ (CJC), 6♂ (NMNH); Villavicencio, Meta, 1♂ (CJC), 3♂ 2♀ (MNHN); Montanita, Caquetá, 1♂ (CJC), 2♂ (NMNH); Tres Esquinas, Caquetá, 3♂ 2♀ (NMNH); Putumayo, 8♂ (MNHN); Umbria, 1♂ (MNHN); Meta, nr. Villavicencio, 1♂ (NMNH). ECUADOR: Rio Jondachi, 1♂ (CJC); Puyo Pastaza 2♂ (CJC), 2♂ (NMNH); Cotundo Napo, 2♂ (CJC), 4♂ 1♀ (NMNH), 2♂ (NMNH); Limoncocha 3♂ (NMNH). PERU: Tingo Maria, 3♂ (CJC); Chanchamayo, 2♂ (NMNH); Iquitos, 2♂ (NMNH), 1♀ (MNHN), 6♂ (MNHN); Chanchamayo, 4♂ 2♀ (MNHN); La Merced, 2♂ 2♀ (MNHN); Rio Tono, 4♂ 2♀ (MNHN); Jepelacio, 1♂ (MNHN); Rio Perene, 3♂ (MNHN); Huancabamba, 1♂ (MNHN); Madre de Dios, 1♂ (MNHN).

Euselasia cyanira Callaghan, new species

(Figs. 19–20, 32)

Description. *Male:* legs yellow, palpi and facial sutures white; forewing length of holotype 22 mm (range of material examined 20–22 mm, $n=7$); dorsal surface of forewing ground color black, costal margin purple-blue from base to end of cell, continuing as a 4 mm wide lighter blue band to anal angle; hindwing ground color black, costa light brown, 2 mm wide marginal blue band from M_1 to anal angle; ventral pattern shows through to dorsal surface; ventral surface light grey with a light blue sheen, stronger at the anal angle; on forewing, band 1 is absent; bands 2–4 red/brown and parallel; band 5 broken into three arrow shaped spots in cells R_3 – R_4 , R_4 – M_1 and M_1 – M_2 , continuing as a wide band from M_2 to 2A, then as a thin line at an angle basad to the inner margin; band 6 distinct, reaching CU_2 ; margin light brown with black fringe; hindwing bands 2–4 are continuations of those on the forewing from costa to 2A; bands 2 and 3 slightly concave to the base; band 5 consists of elongated arrow-shaped spots pointing basad, two each in cells CU_1 – CU_2 and CU_2 –2A and the rest with one each, except cell M_2 – M_3 which contains an oval, black ocellus separated from line 3 by a yellow shading 0.87 mm wide and bordered distad by a short, white line; margin light grey with a 1 mm wide orange line distad, and a thin black line at base of fringe. *Female:* unknown.

Types. *Holotype:* male, with label "Pumayacu, Huallaga, Peru," and a red TYPE label. *Paratypes:* six males from Manaus, Amazonas and U. Putumayo, SE Colombia. The holotype and two paratypes are in the Museum d'Histoire Naturelle, Paris; one paratype is in the collection of the author; material will be distributed to the Museo Nacional, Rio de Janeiro and the USNM, Washington, D.C.

Genitalia. As illustrated (Fig. 32).

Geographical Variation. *Euselasia cyanira* ranges from Manaus, Brasil to Putumayo, Colombia then to central Peru, always in humid tropical lowland forest. All specimens examined are similar in appearance, suggesting that the species is quite uniform over its range.

Diagnosis. The dorsal surface of *E. cyanira* resembles closely that of *E. eutychnus* with

broader blue bands on the forewings. However, *E. cyanira* may be easily separated by its white rather than yellow facial sutures. Although the ventral surface of *E. cyanira* resembles that of *E. clithra*, hindwing bands 2 and 3 are slightly concave to the base in *E. cyanira* and straight in *E. clithra*. The wider blue band on the forewing of *E. cyanira* separates it from *E. clithra*.

Euselasia clithra (Bates 1868)

(Figs. 21–24, 33, 38)

=*E. clithra jugata* Stichel 1919, new synonym

Nomenclature. *Euselasia clithra* was described from a male captured in "Para, L. Amazonas" by H. W. Bates. The type specimen is in the British Museum (Natural History).

Geographical Variation. *Euselasia clithra* shows considerable clinal variation over its range from eastern Pará to the foothills of the Andes south of the Amazon and Rio Negro rivers. The males from Pará, nominate *E. clithra*, are characterized by ventral hindwing bands 2 and 3 diverging from band 4 toward the inner margin, leaving a wide, open space of white scales between them. To the west, the lines become increasingly closer together until they are nearly parallel (*jugata* Stichel 1919, described from Rio Jurua, Brazil). The dorsal surface invariable. Females tend to be slightly darker in the western portion of the range.

Ecology and Behavior. In my experience, *E. clithra* inhabits the terra firme forest where the males perch at the edges of treefalls and small clearings in the late morning and early afternoon hours. Adults rest near the ground under sunlit leaves with wings closed. I have never found them common, especially the females, but judging from the long series in museums, at times they may be encountered more frequently.

Material Examined. BRAZIL: Cuiabá-Santarem km 1666, Pa, 2♂ (CJC), 1♂ (NMNH); Ariquemes, RO, 1♂ (CJC); Manicoré, Am, 1♂ (CJC), 2♂ (MNHN); Tapajós, Pa, 1♂ (MNHN); Monte Cristo, Pa, 1♂ (MNHN); Itaituba, Pa, 1♂ (MNHN); Altamira, Pa, 1♂ (MNHN); Barreiras, Pa, 4♂ (MNHN); Conceição, Pa, 8♂ 2♀ (MNHN); Amazonas, 1♂ (MNHN); Massauary, Rio Negro, Am, 1♂ (MNHN); Uypiranga, Am, 2♂ (MNHN); São Paulo de Olivença, Am, 1♂ 1♀ (MNHN); Rio Como?, 1♀ (MNHN); Manacapuru Rd., south of Manaus, Am, 1♂ (CJC). PERU: Pakitza, 20♂ 3♀ (NMNH); Iquitos, 4♂ (MNHN); Amazon Supl., 1♂ (MNHN); COLOMBIA: Putumayo, 6♂ 1♀ (MNHN); Umbria, Putumayo, 1♀ (MNHN).

Euselasia phedica (Boisduval 1836)

(Figs. 25–28, 34, 39)

Nomenclature. Boisduval named *E. phedica* from a male illustrated from French Guiana. The type is in the British Museum (Natural History).

Geographical Variation. There is no variation over the range of this species from French Guiana through the Amazon drainage north of the Amazon river to southern Venezuela. A male in the MNHN collection from "Putumayo" may be mislabeled.

Ecology and Behavior. I have no personal experience with this butterfly. However, K. Brown (pers. comm.) says that it inhabits deep primary forest, perching close to the ground under leaves on the edge of treefalls.

Material Examined. FRENCH GUIANA: Bas Maroni, 6♂ (MNHN); St. Laurent, 1♂ (MNHN); St. Elie, pk 15.5 on D21, 2♂ (NMNH); St. Jean, Maroni, 2♂ (NMNH). VENEZUELA: Cerro de Neblina, Basecamp, 140 m, 1♀ (NMNH). BRAZIL: Ypiranga, Am, 1♂ 1♀ in cop. (MNHN); Manaus, Am, 1♂ (MNHN); Obidos, Pa, 1♂ (MNHN); Rio Umary, 4♂ (MNHN). COLOMBIA: Putumayo, 1♂ (MNHN)(?).

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TERMINATION OF PUPAL DIAPAUSE IN *CALLOPHRYS* *SHERIDANII* (LYCAENIDAE)

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ABSTRACT. When *Callophrys sheridanii neoperplexa/newcomeri* pupae were incubated at 4°C for 100 days, 65% of the pupae eclosed within 8 days and the remaining 35% eclosed gradually 45 to 200 days after the termination of the chilling. Non-chilled pupae stopped their development at the eye pigmentation stage. More than 60% of adult eclosion was observed within 30 min after lights on. These results suggest that adult eclosion of this species occurs abruptly in the early morning on the first few warm days in spring, and one of the factors explaining the sporadic late records in the field is the gradual termination of the pupal diapause.

Additional key words: circadian rhythm, eclosion, low temperature, endocrinology.

Insect development is governed primarily by ecdysteroids and juvenile hormone (JH). Prothoracicotropic hormone (PTTH) from brain neurosecretory cells stimulates prothoracic glands to secrete 3-dehydroecdysone in *Manduca sexta* L. (Sphingidae) (Warren et al. 1988), it is then converted to ecdysone and then to an active hormone, 20-hydroxyecdysone, which initiates development (Rees 1989). Ecdysteroids initiate the larval molt in the presence of JH secreted from corpora allata. In the last instar larva in Lepidoptera, a small peak of ecdysteroids in the absence of JH causes the cessation of feeding, larval-pupal commitment of the epidermis, and the onset of wandering behavior. Subsequent exposure to ecdysteroids initiates pupation in the presence of JH (Riddiford & Hiruma 1990). This JH in the wandering stage is important to coordinate PTTH release (Hiruma 1986) and subsequently it stimulates prothoracic glands to secrete ecdysteroids that are responsible for pupation, in addition it prevents to become an adultoid (a pupa with some adult structures) in some lepidopteran species (see Hiruma 1980). Adult development is caused by an ecdysteroid surge in the pupal stage in the absence of JH (see Riddiford & Hiruma 1990 and Nijhout 1994 for reviews).

Pupal diapause is characterized by the failure of the ecdysteroid secretion from prothoracic glands after pupation, which is primarily due to the failure of the release of PTTH from brains (Williams 1946, 1947, Denlinger 1985). The brain of a diapausing pupa can be activated to secrete PTTH by chilling, thus terminating diapause so that adult development is initiated (Williams 1952).

Callophrys sheridanii Edwards (Lycaenidae) is widely distributed in the western U.S., and differentiated to several different subspecies (Scott 1986). In Washington State, there are two subspecies distinguished: *C. s. neoperplexa* Barnes and Benjamin occurring in the Columbia Basin and adjoining regions, and *C. s. newcomeri* Clench occurring in the south, southeast, and the east slope of the Cascade Mountains. The two intergrade in the east central Cascades, from lowland steppe to high mountains in Kittitas and Chelan Counties west of the Columbia River (Pelham & Hiruma, pers. obs.). This species is considered univoltine and enters obligatory diapause in the pupal stage for hibernation (Scott 1986).

In this paper, we show that diapause intensity in *C. s. neoperplexa/newcomeri* pupae is heterogeneous and the timing of the adult eclosion responds to photoperiod. Also, we discuss the relationship between the results obtained in the laboratory and those of field observations.

MATERIALS AND METHODS

Eggs and first instar larvae of *Callophrys sheridanii neoperplexa/newcomeri* were collected from *Eriogonum compositum* Dougl. (var. *leianthum* Hook.) (Polygonaceae) in Schnebly Coulee, Kittitas County, Washington, and some of the eggs were laid in the laboratory on *E. compositum* by females caught in the same location. All the field caught eggs and larvae were brought into the laboratory, and reared under crowded conditions on *E. compositum* leaves in a plastic dish (14 cm diameter/2 cm height) at 26°C in a 17L:7D photoperiod. Twenty to 30 larvae were reared together until third instar larvae, then reduced the numbers to 10 to 15 in the fourth instar larvae. The leaves were changed daily. The food plant was wrapped with plastic bags and kept at 4°C no longer than 2 weeks. Lights off, the beginning of a new day, was set at 00:00 AZT (Arbitrary Zeitgeber Time) (Pittendrigh 1965). In this condition, cannibalism in larvae of this species was not observed as observed in the closely related European species, *Callophrys rubi* L. (Lycaenidae) (Ford 1945).

Pupae were kept at 26°C in a 17L:7D photoperiod for 67 to 77 days after pupation, they were then transferred to a 4°C incubator for 100 days at dark, followed by transferring back to the 26°C condition (17L:7D). Non-chilled pupae were kept at 26°C at dark for 100 days instead of placing at 4°C, then at 26°C in a 17L:7D condition. Adult eclo-

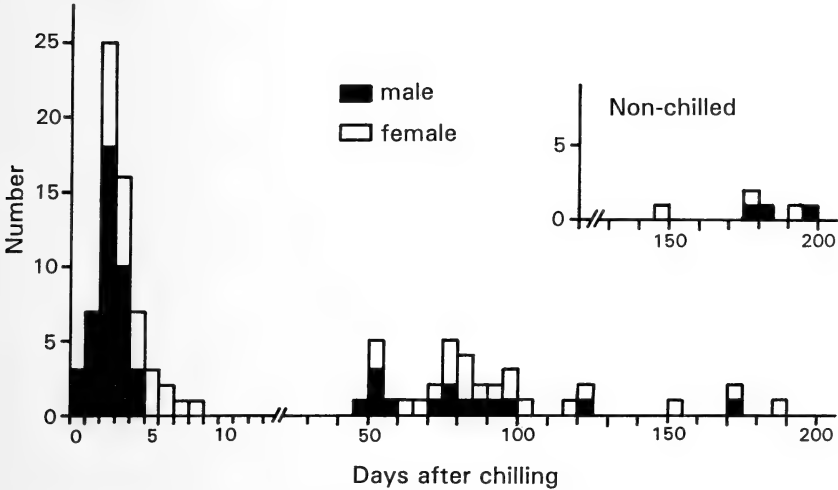


FIG. 1. Adult eclosion from *Callophrys sheridanii neoperplexa/newcomeri* pupae. Pupae were kept at 26°C for 67 to 77 days after pupation, they were then transferred to 26°C condition 100 days after the incubation at 4°C (n = 122). One male eclosed and 2 pupae died at 4°C. Nineteen pupae died after the chilling, but 15 developed to adult inside of the pupal cuticles and died without eclosion, probably because of desiccation. As a control, pupae (n = 50) were kept at 26°C throughout the experiments (see Materials and Methods), and the days of eclosion were calculated as 0 at the time of the termination of the chilling in the experimental (inset). Only 6 eclosed, and one developed to adult but did not emerge ("150 days" is equivalent to "327 days after pupation"). The rest of them died by desiccation without forming any scales. Dead pupae were excluded from the data.

sion was checked daily for about 400 days after pupation, and dissected all the non-eclosed pupae to examine whether or not they died.

RESULTS

Time of eclosion of diapausing pupae. All pupae developed to the stage to which compound eye pigmentation occurred within 67 to 77 days at 26°C in a 17L:7D photoperiod, then stopped their development (n = 202). Most of the pupae produced very audible creaking sounds when disturbed as reported in many lycaenid pupae (Downey 1966, Brakefield et al. 1992), which was predicted by the presence of the stridulating organ in *C. sheridanii* (Downey 1966). The sound was produced from shortly after pupation to the beginning of the eye pigmentation stage.

Figure 1 shows that if pupae were not exposed to 4°C, only 12% of the pupae eclosed (6 out of 50) 326 to 377 days after pupation, which were equal to 149 to 200 days calculated as days after chilling (see below). When pupae were placed at 4°C for 100 days, the adult eclosion

occurred in 65% of the pupae within 8 days after the termination of the chilling. One male eclosed even at 4°C. The remaining 35% eclosed gradually over about 200 days after chilling (Fig. 1). Apparently, the pupal diapause was terminated by the incubation at 4°C, and the diapause intensity of this population is not homogenous. This pattern of adult emergency indicates that there are at least two physiologically different pupae in the population. One is very sensitive to a low temperature to break diapause and adult eclosion occurs within 10 days after the termination of chilling (group 1), and the other is much less sensitive to a low temperature whose adult eclosion occurs 50 to 100 days after the termination of chilling (group 2). Since non-chilled pupae did not emerge more than 140 days (Fig. 1), the adult eclosion of the group 2 pupae is considered to have responded to the chilling.

Sex ratio. Sixty-four percent (42 of 66) of adults were male in the group 1, but only 39% (16 of 41) in the other groups (Fig. 1). Male ratio was statistically higher in group 1 ($P < 0.001$), but female ratio was statistically higher in the others ($P < 0.003$). The overall sex ratio (male/male + female) of the adults in the laboratory reared population was 0.542 and it was not significantly different at $P > 0.05$ ($n = 107$). According to the records deposited in the Burke Memorial Museum of the University of Washington and those of our private collection, males were more commonly caught than females in the gulch bottom of Schnebly Coulee, where the food plant occurs, in mid March to mid April, and the sex ratio was 0.77 ($n = 188$) (significantly different at $P \ll 0.001$).

Timing of adult eclosion. Of the adults that emerged 1 to 5 days after chilling, more than 60% did so within 30 min after lights on (Fig. 2). This indicates that adult eclosion most likely occurs in the early morning in the field.

DISCUSSION

The duration of diapause under well-defined environmental conditions usually is quite consistent for a given population, and the insect's capacity to respond to environmental cues can also be directed by its genetic potential, sex, food plants and maternal history (Denlinger 1985, Pratt & Ballmer 1993). Diapause termination is linked directly to a specific environmental cues, and the exposure to a low temperature was one of the main factors in *C. s. neoperplexa/newcomeri* (Fig. 1). Yet the trait is quite polymorphic for the termination as found in *Hyalophora cecropia* L. (Saturniidae) (Waldbauer & Sternburg 1973) whose bimodality for the termination of the pupal diapause has a genetic basis. Figure 1 suggests that the population of *C. s. neoperplexa/newcomeri* is genetically heterogeneous, which also is evidenced by the mixed degrees of the postmedian line. The similar bimodal adult emergence was

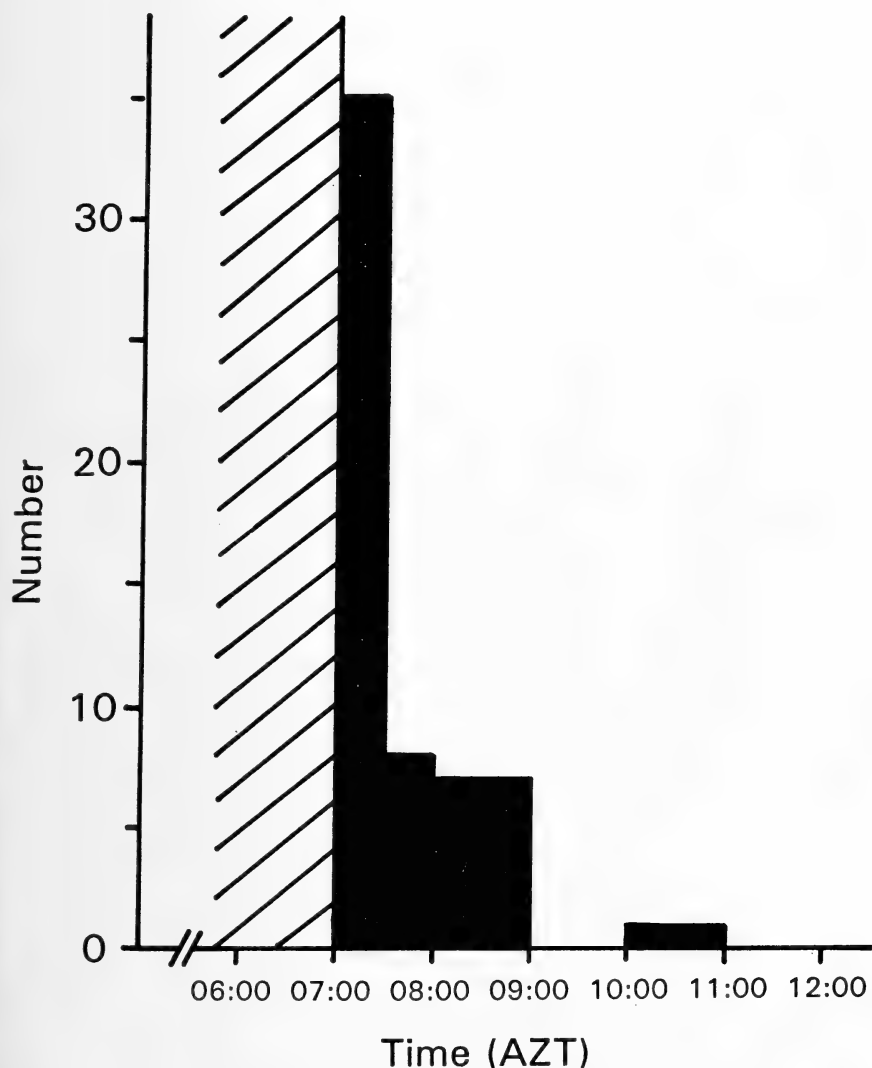


FIG. 2. Distribution of adult eclosion for *C. s. neoperplexa/newcomeri* under 17L:7D. Observations were performed on adults eclosed 1 to 5 days after the termination of chilling ($n = 58$). Seven adults eclosed during the dark.

also observed in the laboratory reared *Incisalia mossii mossii* Edwards (Lycaenidae) (Hiruma, unpubl. data).

The developmental stage of the arrest of diapausing pupae varies among species. In *M. sexta* (Bell et al. 1975, Bowen et al. 1984) and *H. cecropia* (Williams 1946), pupae enter diapause shortly after pupation

due to the inactivation of the brains, whereas in *Luehdorfia japonica* Leech (Papilionidae), an univoltine species, the pupae complete almost all adult development by the beginning of winter. Yet adult eclosion does not occur until the following spring (Hidaka et al. 1971). It is interesting that pupal development occurs up to a certain level before the onset of diapause in *C. s. neoperplexa/newcomeri*. Probably, the brain-prothoracic gland axis is still active to secrete ecdysteroid even after pupation, so that the pupal development occurs until eye pigmentation stage. The determination of PTTH and/or ecdysteroid titer in the hemolymph is necessary to ascertain this hypothesis.

Adult eclosion occurs at specific times of day in *M. sexta*, *Antheraea pernyi* Guérin-Ménéville (Saturniidae) and *H. cecropia*; it is controlled by a circadian clock and has been classified as a "gated" event (Truman 1985). For the gated adult eclosion in *M. sexta*, the brain contains the clock that determines when eclosion hormone release will occur. The adult eclosion of *C. s. neoperplexa/newcomeri* also is thought to be controlled by a biological clock, and this may be due to the release of eclosion hormone shortly after lights on.

According to our results reported in this paper, more than a half of the pupal population of *C. s. neoperplexa/newcomeri* at a given location must emerge in the early morning on the first few warm days in Spring, followed by sporadic emergence throughout summer. Our field observation partially supports this hypothesis. Adults of this species fly in early March to mid April in the lowland steppe such as Schnebly Coulee (500 m), but the peak of the flying period of fresh adults in each year is usually 7 to 10 days (Hiruma & Pelham, pers. obs.), which is supported by the outbreak of the eclosion of the diapausing pupae shortly after the termination of chilling (Fig. 1). In the higher elevations such as Chumstick Mountains (1600–1700 m) in Chelan County, Washington, and Reecer Creek Road (1400 m) in Kittitas County, Washington, adults appear in early April to early May (depending on the snow melt), but there are sporadic late records in both locations. In Schnebly Coulee and its vicinity, a relatively fresh female specimen was caught on 7 May 1988, two males on 16 May 1987 and a male on 20 May 1984 (we did not find any adults in mid April in these years), and in the Chumstick Mountains, a fresh female on 16 July 1991 (Hiruma & Pelham, pers. obs.). Similar late records have been reported many times in *C. rubi*, and it is debatable whether or not these late records are due to second generations (see Ebert & Rennwald 1991 for detailed discussions). Based on our results, these late records are most likely due to the gradual eclosion depending on the diapause intensity, although we cannot rule out the possibility of second generations.

Sexual differences in diapause response is common (see Denlinger

1985 for examples), and *C. s. neoperplexa/newcomeri* seems to exhibit this feature. Males were more common than females in the field, which may be due not only to collecting efficiency, but also to fewer eclosions of females in spring. It is well known that a certain percentage of diapausing pupae in some species of *Anthocharis* (Pieridae) and *Atrophaneura* (Papilionidae) do not emerge in the expected year after hibernation, but emerge in the same season 2 to 3 years later (Kawazoé & Wakabayashi 1976). It has been reported as an extreme example in *Eriogaster lanestris* L. (Lasiocampidae) that the adult eclosion of 15 pupae occurred 14 years after pupation (Van-Nuvel 1976), although a 7-year-diapausing period was frequently observed in this species (South 1907, Van-Nuvel 1976). This seasonal adaptation has a number of advantages for unexpected unfavorable environments. In *C. s. neoperplexa/newcomeri*, the genetic program may not be completed to do so, and as a result it causes gradual adult eclosion during the same year.

These results indicate that results obtained in the laboratory are able to explain some of the unsolved observations in the field, and therefore both types of research will help to analyze ambiguous results.

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NOTES ON THE MALE GENITALIA OF THE *ANAEA RYPHEA* - *ANAEA EURYPYLE* COMPLEX (NYMPHALIDAE)

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ABSTRACT. *Anaea ryphea* resembles closely *Anaea eurypyle*, and both are found over the same geographic range. Separation of the two species has been based on two external characters that vary continuously and unimodally. Genitalic dissections of 20 males with the traditional *A. ryphea* wing pattern and 20 males with the *A. eurypyle* wing pattern showed that male genitalic characters vary similarly in both taxa. There appears to be no consistent association between male genitalia and wing pattern variation in the *A. ryphea* - *A. eurypyle* complex. I conclude that the genitalic characters within this complex vary greatly and that no consistent "ensemble" exists that separate the taxa called *A. ryphea* and *A. eurypyle*, and these two "species" seem to be nothing but artificially designated variants along gradients of continuous variation within a single, geographically widespread, species.

Additional key words: *Fountainea*, intraspecific variation, *Memphis*, wing pattern.

The genus *Anaea* (*sensu lato*) is very confusing and confused (see D'Abrera 1988). There is no cladistic treatment of it, and several of its species need careful reexamination. In the comprehensive revision of Comstock (1961) the genus contained 119 species, distributed in several subgenera. The species that were then assigned to subgenus *Memphis* are currently in three genera: *Anaea*, *Memphis* (DeVries 1987), and *Fountainea* (Rydon 1971, D'Abrera 1988).

Anaea ryphea Cramer (= *Memphis ryphea*, = *Fountainea ryphea*) resembles closely *Anaea eurypyle* C. and R. Felder (= *Memphis eurypyle*, = *Fountainea eurypyle*) (Caldas 1994). They occur over similar geographic ranges, from Mexico to Argentina and southern Brazil, although according to Comstock (1961) the two taxa overlap only from Mexico to Bolivia. He had no records of *A. eurypyle* from the Amazonian region or Brazil, but specimens from these regions can be found in other collections (A. Caldas, pers. obs.). Although the two species have been separated by external characters, analyses of 499 males from localities throughout their geographic range showed that the two main external characters used to distinguish the species (the length of the "tail" on the hind wing and the degree of irregularity of the "mesial" line on the underside of the hind wing) vary in a continuous and correlated way, but with unimodal frequency distributions (Caldas 1996). One extreme of these distributions—long tail and straight "mesial" line—diagnoses the species *A. eurypyle*, and the other extreme plus the mode—short or no tail, irregular "mesial" line—diagnoses *A. ryphea*. However, many intermediate states exist. This variation is suggestive of a single species.

According to Comstock (1961), the male genitalic armature is consis-

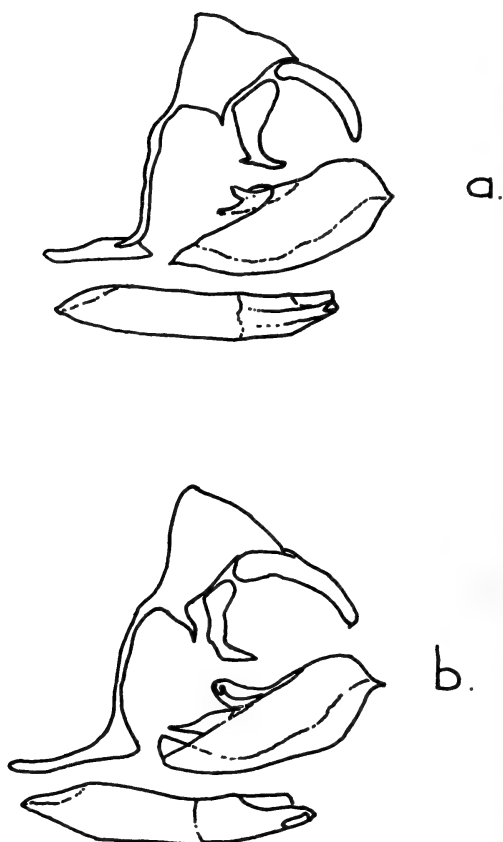


FIG. 1. Original drawings of (a) *Anaea ryphea* and (b) *Anaea eurypyle* male genitalia, after Comstock (1961). Scale bar = 1 mm.

tently different between the two species. He provided line drawings of their genitalia (Fig. 1) to illustrate the main differences in the shape of the gnathos, valvae, aedeagus, and processes of the tegumen, but gave no further details in the text. Previously, however, Johnson and Comstock (1941) had stated that "the structure of the gnathos in *ryphea* separates it from all others of the group. The presence of tubercules [sic] in the central surface is unique."

Since the external morphological characters previously examined by

me (Caldas 1996) could not be used for distinguishing taxa in this complex, because of their unimodal distribution, I sought to determine whether genitalic characters could distinguish species. I compare my findings with the drawings in Comstock (1961).

MATERIALS AND METHODS

I dissected the genitalia of 20 male specimens with the wing pattern characteristic of *A. ryphea* and 20 specimens with the *A. eurypyle* pattern from the collection of the National Museum of Natural History, Smithsonian Institution. Specimens were from Peru, Brazil, Bolivia (both taxa), Colombia, Panama (*A. ryphea*), Mexico, Honduras, and Costa Rica (*A. eurypyle*). There were no individuals representative of the whole geographic range for either species. My goal was to identify which structures, if any, could distinguish the two taxa. Dissections were made in water, under a stereomicroscope, after washing the separated abdomens in alcohol (EtOH) and boiling them for 3.5 minutes in 10% potassium hydroxide (KOH). Genitalia were kept in vials with glycerine.

RESULTS AND DISCUSSION

Male genitalic characters vary similarly in both taxa, and no consistent trend was observed for the structures that Comstock (1961) used to separate *A. ryphea* and *A. eurypyle*. No two individuals with identical genitalia were found among the 40 males dissected. Some of the variation is illustrated in Figs. 2 and 3, which show randomly selected genitalia. These are drawings made in the same schematic way of the original drawings of Comstock (1961), in order to facilitate comparison with Fig. 1. Comparing the genitalia of three individuals with *A. ryphea* external characteristics (Figs. 2a, 2b, and 2c) with Comstock's drawing (Fig. 1a), the latter appears to be inaccurate. No individual with an *A. ryphea* wing pattern was found to have a small ventral spine on the tegumen, anterior to the gnathos; all had it long, as in Fig. 1b. The gnathos did not present the shape illustrated in Fig. 1a, nor did the valvae. Similarly, the aedeagus and saccus varied in shape and size throughout the complex (Figs. 2a, b, and c, no two aedeagi or sacci with the same shape).

The genitalia in Figs. 3a, 3b and 3c cannot be considered different from those in Fig. 2, although they all belong to individuals with the *A. eurypyle* wing pattern. Again, they do not agree with Comstock's drawing of *A. eurypyle* genitalic armature (Fig. 1b). No individual has the slender gnathos, the valvae vary in shape and length, as does the aedeagus (Figs. 3a, b, and c). They bear the same long spine-like process of the tegumen shown in Figs. 2a, b, and c. In fact, the genitalia in Figs. 2 and 3 seem to be a mixture of characteristics from both Comstock's drawings.

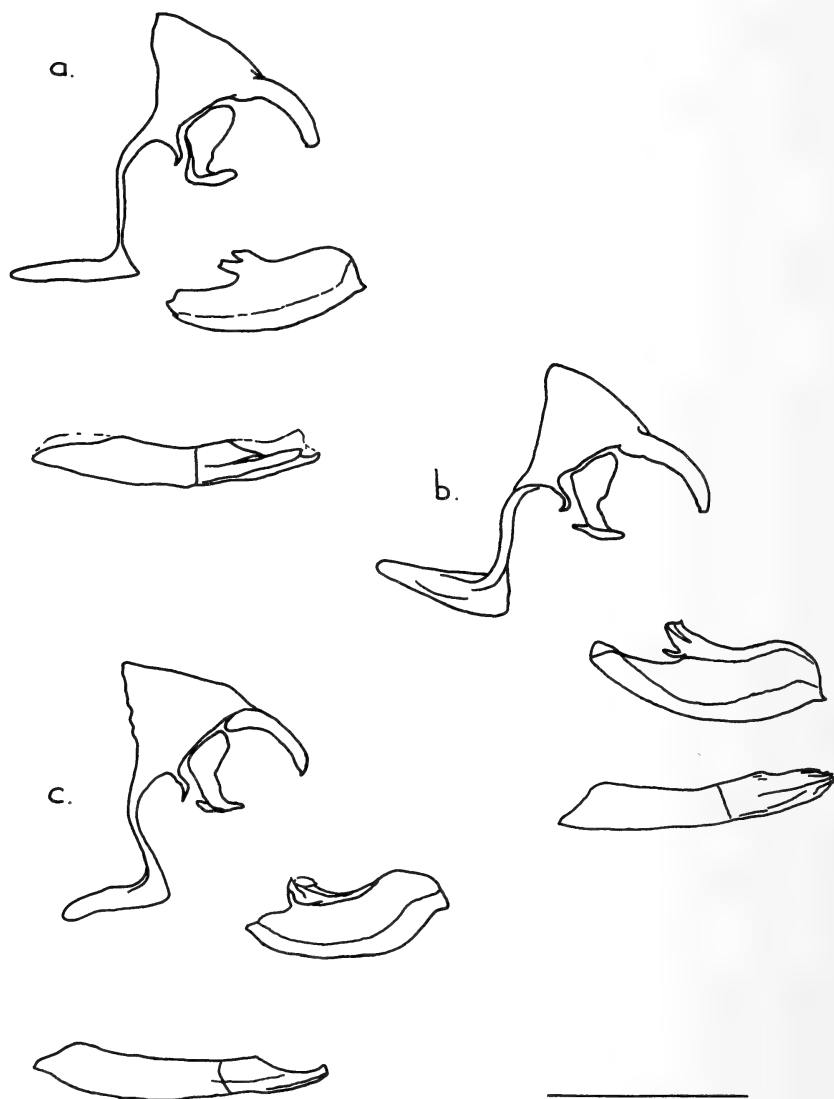


FIG. 2. Genitalia of male individuals with *Anaea ryphea* wing pattern, respectively from (a) Panama, (b) Peru, (c) Brazil. Scale bar = 1 mm.

Part of the difference seen by Comstock in the genitalia of *A. ryphea* and *A. eurypyle* may be due to the angle from which the genitalia were seen. He probably used slides of genitalia (F. Rindge, pers. comm.) to make his drawings, and slide mounting is likely to alter the shape of genitalia. Figs. 4 and 5 show photographs of the same genitalia from

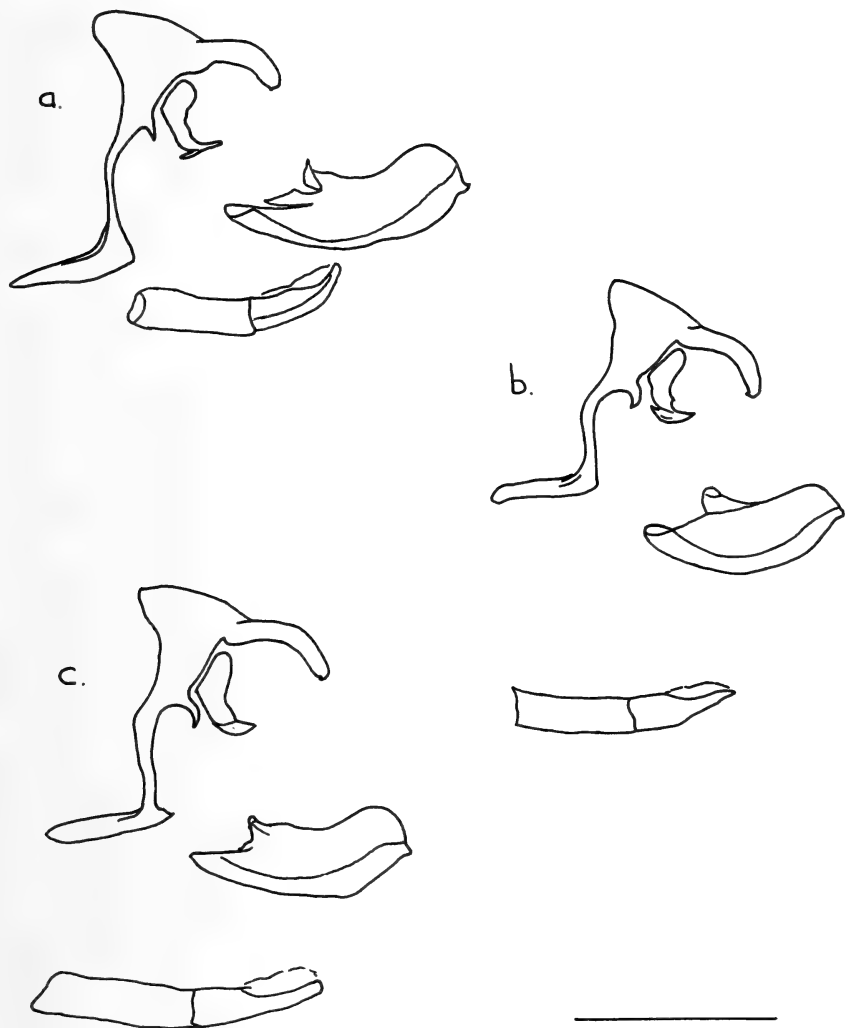
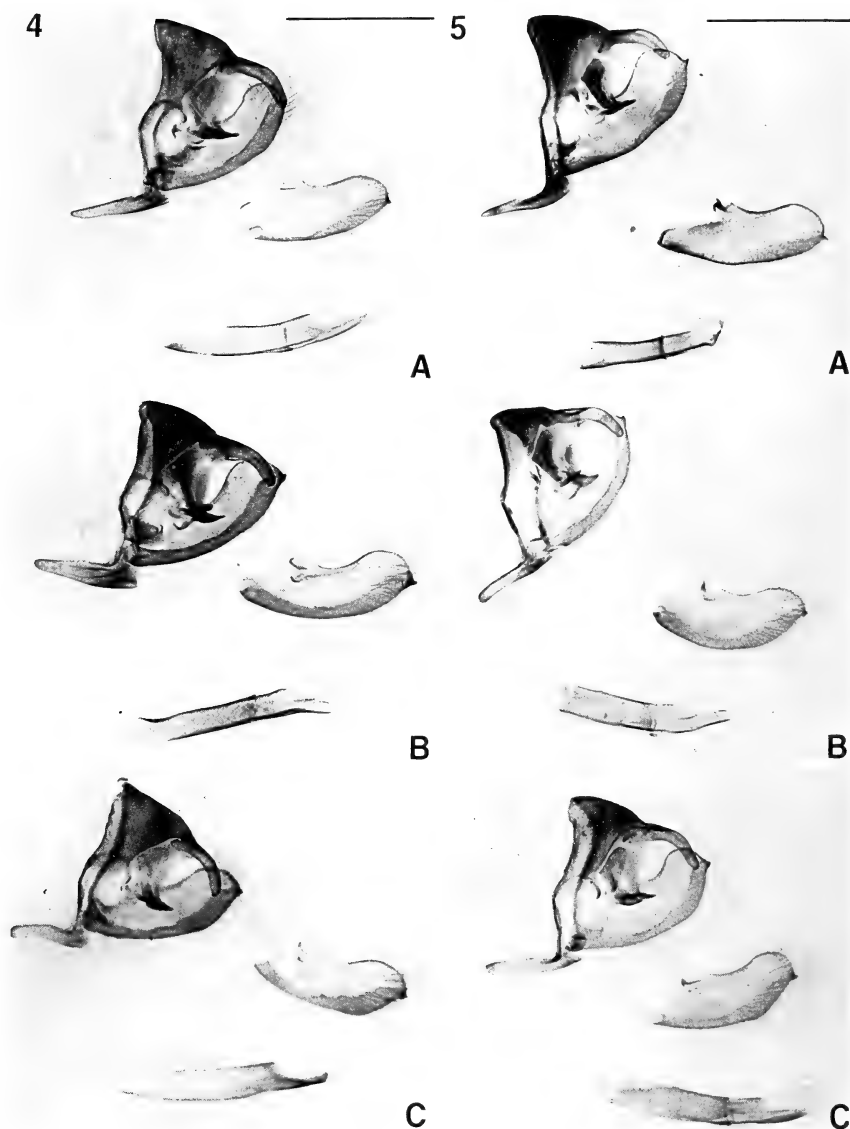


FIG. 3. Genitalia of male individuals with *Anaea eurypyle* wing pattern, respectively from (a) Bolivia, (b) Brazil, (c) Mexico. Scale bar = 1 mm.

Figs. 2 and 3, taken from an angle different from the one used for the drawings (all drawings were made with the genitalia lying flat so that the superior or left side matched the inferior or right side). Thus, the gnathos appears slender (4c and 5a) or broad (4a and 5c). The uncus can appear shorter (5a), the same length (4a) or longer than the tegumen (5b). The tegumen itself always bears a long spine-like process beneath the gnathos, although Comstock's drawing for *A. ryphea* (Fig. 1a) shows



FIGS. 4-5. Male genitalia photographs. 4, male genitalia from individuals with *Anaea ryphea* wing pattern; 4a, b, and c (top to bottom) refer to drawings 2a, b, and c respectively. 5, male genitalia from individuals with *Anaea eurypyle* wing pattern; photographs 5a, b, and c (top to bottom) refer to drawings 3a, b, and c respectively. Scale bar = 1 mm.

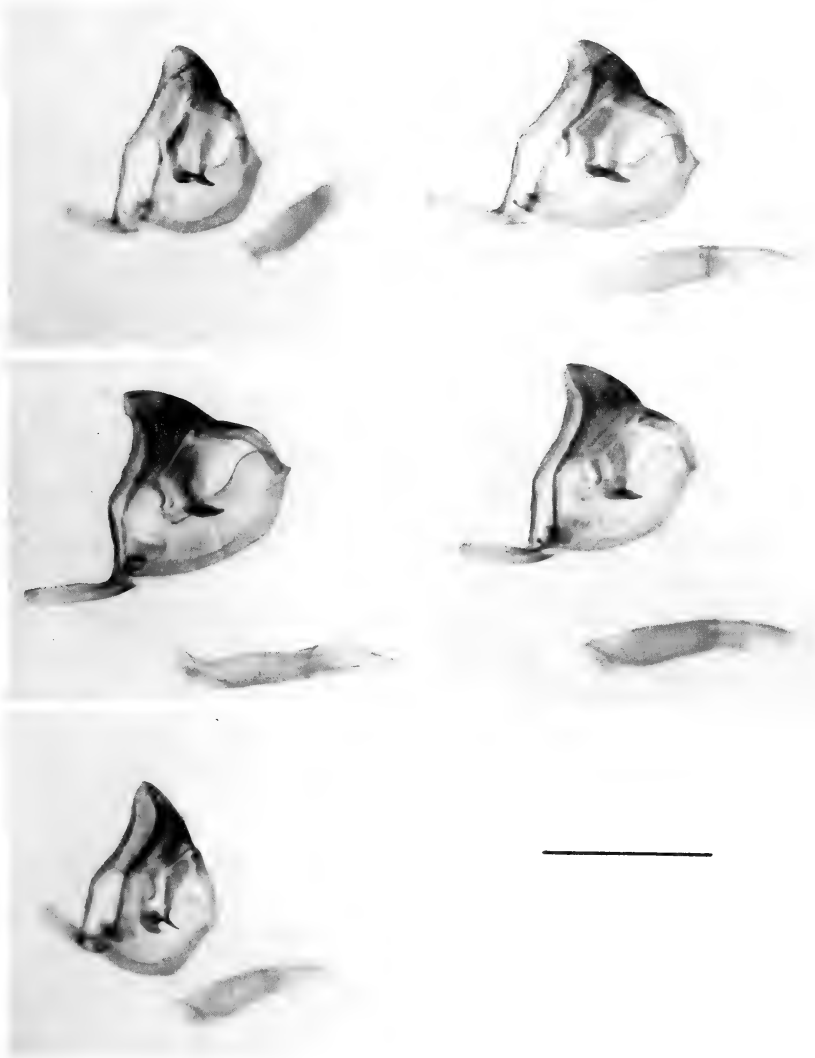


FIG. 6. Genitalic armature 3c/5c shown from five different angles (6a to 6e, starting on top left). Scale bar = 1 mm.

a small process. Shape and size of the valvae vary greatly. Again, the six genitalia in Figs. 4 and 5 show that no two valvae are completely similar.

While taking the previous photographs, I noticed that a slightly different angle sometimes provides very different views of the same armature. To further illustrate my point, I decided to have photos of the same genitalic armature taken from different angles. Thus, Figs. 6a–6e

are all from the same armature shown in Figs. 3c and 5c. As the angle varies, the gnathos can appear more (6a, 6b, 6e) or less slender (6c, 6d), the proportion of the uncus in relation to the tegumen varies—tegumen longer than the uncus, Fig. 6c (compare with 1b), or shorter than the uncus, Figs. 6b, 6d (compare with Fig. 1a)—and the aedeagus can appear as in Fig. 1a (Fig. 6c) or 1b (Fig. 6d), both Comstock's illustrations. This reinforces my idea that the variation shown in the latter may be partially due to the angle from which the genitalia were seen. Of course, Figs. 6a and 6e are extremes, but they show very well how slender the gnathos can appear.

I conclude that the genitalic characters within this complex vary greatly and that no consistent "ensemble" exists that separate the taxa called *A. ryphea* and *A. eurypyle*. These results, together with the results of my previous studies (Caldas 1996), suggest that these two "species" are nothing but artificially designated variants along gradients of continuous variation within a single, geographically widespread, species. Another species in the group—*Anaea ecuadoralis*, which resembles *A. ryphea* and *A. eurypyle* closely in many features—may also be part of this variable species.

ACKNOWLEDGMENTS

I thank the Smithsonian Institution, which, through its curators, allowed the development of this research. John M. Burns, Donald Harvey and Robert K. Robbins offered suggestions and held helpful discussions throughout the project. I especially thank Elizabeth Klafter, who provided most logistic and technical support I needed, and Carl C. Hansen, for that extra effort with the photographs. This research was funded by two CAPES/Ministry of Education/Brazil grants, a Smithsonian short-visit grant, and several SR-2/Universidade do Estado do Rio de Janeiro fundings.

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GENERAL NOTES

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BODY WEIGHT AS RELATED TO WING MEASURE IN HAWKMOTHS (SPHINGIDAE)

Forewing or hindwing length (L) and forewing span (S) are often used as species body-size indices in Lepidoptera, but the body weights (W) actually represented are not usually known. Establishing mathematical relations between total body weight or mass and wing measure among species of a taxon not only validates the use of wing measure as a body size surrogate (Miller 1996), but also enables estimation of body weight from wing measure for physiological and ecological purposes. In detail, such relations are specific for different groups; in form, they are usually allometric power functions of $W = a (L^b \text{ or } S^b)$ or the logarithmic equivalent (Miller 1977). Wing length is defined here as the distance between the wing base (excluding tegula) and the farthest extending wing tip (including fringe); wing span is defined as the farthest distance between the wing tips on specimens spread in the usual manner.

In their studies of flight mechanics, Bartholomew and Casey (1978) and Casey (1976) assembled and tabulated W and L values for 15 and 38 identified hawkmoth species, respectively. Although they did not derive relations between W and L in the foregoing papers, Casey (1989) presented such a relation later. This relation had L rather than W as the dependent variable, was based on only the smaller of the above data sets, and was displayed on

Live body wt. (g) (W)

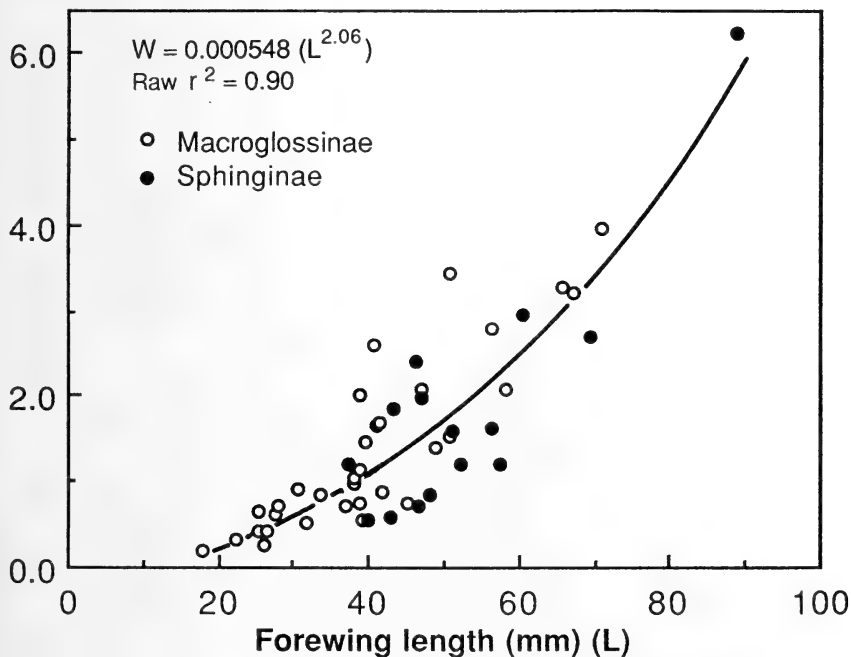


FIG. 1. Live body weight as related to forewing length in hawkmoths. Each point represents from one to several individuals of either or both sexes of a species. Data from Bartholomew and Casey (1978) and Casey (1976).

a double-logarithmic scale. Here I recharacterize the relation with W as the dependent variable using both of the above data sets and displaying results on an arithmetic scale.

Study data here are 70 observations on live weight (W), forewing length (L), and forewing span (S) of field-caught individuals of 48 identified species (Bartholomew & Casey 1978, Casey 1976). These species include 33 Macroglossinae and 15 Sphinginae—the sole subfamilies recognized in Sphingidae (Hodges 1971, Pittaway 1993)—and there are 29 New World and 19 Old World species. The sexes are pooled because many individuals originally were not sexed. Species live weights range from 0.18 to 6.25 g, essentially the full range for the family. For display, two or more observations for the same species were averaged. In analysis, species means were weighted by the number of observations. Where only S was originally given for a species, as in the data set of Casey (1976), I derived L after measuring L and S on D'Abrera's (1986) life-size illustrations such that $L = S(L_{D'Abrera}/S_{D'Abrera})$. To solve the equation $W = a(L^b)$, I used the quasi-Newton loss function for ordinary least-squares nonlinear regression (SYSTAT 1992). I derived proportionality functions for interconverting L and S by simple ordinary least-squares regression.

The recharacterized family-level relation between live body weight (W) and forewing length (L) is $W = 0.000548 (L^{2.06})$ (Fig. 1). It is evident from Fig. 1 that sample species of Sphinginae are larger in mean size than those of Macroglossinae, an outcome that may reflect a real condition among hawkmoths. The subfamilies do not seem to differ in the W versus L relation, however. The proportionality functions which serve to estimate L from S and vice versa when one or the other measurement is available but the other desired are $L = -1.09 + 0.467 S$, and $S = 4.46 + 2.094 L$ ($r^2 = 0.98$).

This study reconfirms that hawkmoth body weight is indexed by wing measure. Live body weight increases as the square of forewing length in Sphingidae, whereas it increases as the cube in Tortricidae (Miller 1977). The difference is fundamental, and reflects the empirical nature of such relations and their dependence on morphometrics and physiology.

Live weights estimated from the nonlinear equation with forewing length (Fig. 1) are not intended for rigorous use. Rigorous use would require not only confidence intervals for the equation, but also body-weight controls in the original sources for sex, egg load, and crop content.

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OCCURRENCE OF THE PALAEARCTIC MOTH, *CNEPHASIA LONGANA*
(TORTRICIDAE), ON SANTA ROSA ISLAND, CALIFORNIA

Additional key words: omnivorous leaf-tier, larval competition, Asteraceae, Lamiaceae, Scrophulariaceae.

Santa Rosa Island is the second largest of the eight California Channel Islands, but its Lepidoptera fauna has been poorly known relative to most of the other islands, primarily due to its long term private ownership. Only about 125 species of Lepidoptera were recorded, perhaps 30–40% of an expected total (Powell 1994). Hence, I was not surprised to find 120+ additional species during my first visit, in late April to early May 1995. One of the previously unrecorded species I did not expect was *Cnephasia longana* (Haworth) (Tortricidae: Tortricinae), a Palearctic species that has been known in coastal central California since the 1940s (Powell 1964) but not on any of the Channel Islands.

Cnephasia longana, the so-called 'omnivorous leaf-tier,' was reported in North America in the Pacific Northwest beginning in 1929, where it became a widespread pest of field crops. It was first recognized in California in 1947 (Keifer 1948); within a few years *C. longana* was found widely in the San Francisco and Monterey Bay areas, associated with cultivated and native flowers, strawberries, and other field crops (CDFA records, Middekauff 1949, Powell 1964).

The species is univoltine; winter is passed by first instar larvae in silken hibernacula, and populations are most easily detected by late instar larvae in April and May or adults, which are attracted to lights, from late April to early July, varying with year and locality. First and second instar larvae are leaf miners in low herbs; later instars web terminal parts of the plants, particularly buds and flowers. The species is polyphagous and in California most often feeds on Asteraceae and other herbaceous plants such as poppies, flax, and cultivated flowers, in open field situations (Powell 1964).

Subsequently, *C. longana* has extended its range in California, having been discovered in the Humboldt Bay area (1960), Lake County (1969), San Benito County (1964), and southward, in coastal San Luis Obispo County (1967) and Santa Barbara County at Lompoc (1970) and Goleta (1976) (CDFA records, Essig Museum, R. Priestaf specimens) (Fig. 1).

Scott Miller collected Lepidoptera, including some tortricoids, on Santa Rosa Island in April 1976 and May 1978 and did not take *C. longana* (LACM and SBNHM records). Negative evidence suggests this adventive species was not established elsewhere on the Channel Islands then and in the early to mid 1980s. We did not find adults or larvae on several of the islands: on Santa Cruz Island in May 1984, when a group of four lepidopterists surveyed for microlepidoptera during a four-day visit; C. Drost made many moth collections on Anacapa and Santa Barbara islands during 1985–1988; on the southern islands, we sampled on San Nicolas and Santa Catalina in May 1978; S. Bennett collected extensively on Catalina in 1981–1982; and I collected for a week on San Clemente in April 1980.

On Santa Rosa Island I found males of *C. longana* flying at dawn (0600 PST at 8°C) on the first morning of my visit, and adults appeared abundantly during the following week. They occurred from sea level to the highest peaks (460–480 m), in cattle grazed fields from the east coast to the deflation plane back of the most western coastal dunes. Adults were taken in most blacklight samples, up to 85 in a single trap.

Competitive exclusion by introduced species is a subject that has not been investigated in detail by lepidopterists but may play a role in decline of native species that are near ecological homologues of sympatric immigrants. On Santa Rosa Island I found larvae of *C. longana* numerous in flower heads of four species of Asteraceae: the weed *Achillea millefolium*; a native *Cirsium*, competing with *Platyptilia carduidactyla* (Riley) (Pterophoridae), which probably is introduced on the islands; *Erigeron glauca*, competing with *Platyptilia williamsi* Grinnell; and in two species of *Gnaphalium*, competing with *Tebenna gnaphaliella* (Kearfott) (Choreutidae), *Phaneta apacheana* (Wlsm.) (Tortricidae), *Patagonia peregrina* (Heinrich) (Pyralidae), and *Platyptilia williamsi*. The last three moth

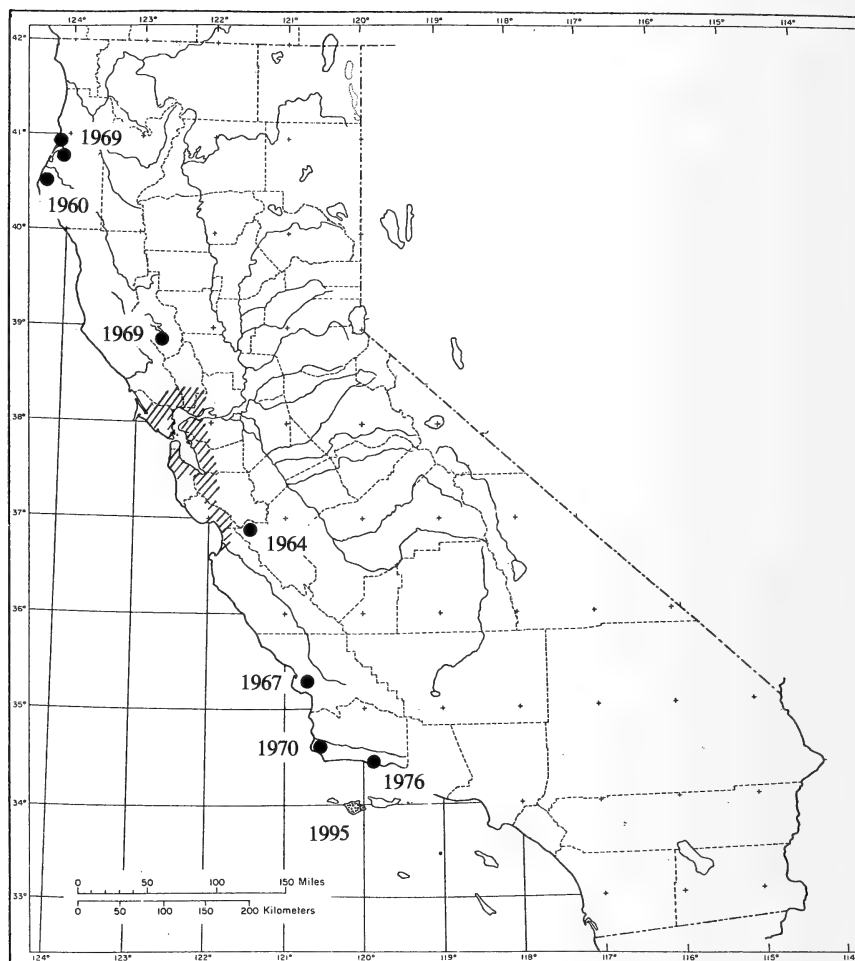


FIG. 1. Distribution of *Cnephasia longana* in California: cross-hatched area indicates the known range in the San Francisco and Monterey Bay areas by 1962; dated localities (solid dots) refer to earliest known records in other areas, and Santa Rosa Island (stippled).

species were encountered commonly on Santa Rosa, while *T. gnaphaliella* was very rare (2 adults), whereas it was abundant on San Clemente Island in April 1980. Larvae of *C. longana* also fed in flowers of *Castilleja affinis* (Scrophulariaceae), where they are potential competitors with *Schreckensteina felicella* (Wlsm.) (Schreckensteiniidae), *Endothenia hebesana* (Wlk.) (Tortricidae), and *Amblyptilia pica* (Wlsm.) (Pterophoridae), which are inhabitants of this plant in coastal central California but are not known on the island. I also found larvae of *C. longana* on *Stachys bullata* (Lamiaceae), the host of *Endothenia conditana* in the San Francisco Bay area.

The omnivorous leaf-tier is a potential competitor with two endemic insular Lepidoptera, *Argyrotaenia franciscana insulana* Powell (Tortricidae) and *Euphydryas editha*

insularis Emmel & Emmel (Nymphalidae). The former is polyphagous, and I collected its larvae on *Achillea* and *Erigeron* on Santa Rosa. The butterfly is a specialist on Scrophulariaceae, and I found the young larvae on *Castilleja exserta* [= *Orthocarpus purpurascens*], which is a likely host of *C. longana*.

I thank C. Mack Shaver, Superintendent, for issuing a permit to inventory Lepidoptera in the Channel Islands National Park, and personnel of the Resource Division, whose cooperation facilitated my visit: Tim Coonan, Heide David, CeCe Sellgren, and David Kushner, particularly the last, who assisted with collections. Tom Eichlin provided copies of early records in the Calif. Dept. Food & Agric., Plant Pest Diagnostics Branch, Sacramento (CDFA records); cooperation by curators of the Los Angeles County Museum (LACM) and Santa Barbara Natural History Museum (SBNHM) enabled use of specimens; and Richard Priestaf provided records of Santa Barbara microlepidoptera.

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EFFECTS OF GENE-ENVIRONMENT INTERACTION ON SILK YIELD IN *ANTHRAEA MYLITTA* (SATURNIIDAE)

Additional key words: tasar silk moth, absolute silk yield, *Terminalia arjuna*, stability.

Antheraea mylitta (Drury) is a saturniid moth of considerable commercial value used for production of tasar silk. Because interactions between genotype and environment may exert significant influence over specific life history features (Falconer 1952, Dickerson 1962, Hanson 1964, Breese 1969), it is likely that silk yield and yield contributing traits in different strains of *A. mylitta* are influenced by seasonal and/or environmental factors (Jolly et al. 1979). In an effort to understand features that may contribute to the maximization of silk production, we conducted rearing experiments to measure the interaction between genotype and environment for silk yield and to screen stable genotypes of *A. mylitta* for use in breeding programs to enhance silk yield.

We investigated eight diverse genetic strains of *A. mylitta*: Nagri₁, Nagri₂, Nagri₃, Sukli, Raily, Sukinda, Laris (P), and Palma. The genotype lines were obtained from the germplasm bank of the Central Tasar Research and Training Institute, Ranchi, Bahir, India. We reared the eight genotypes through two generations in July–August and October–November of 1988. The two generations mature under different environmental conditions: the July–August brood occurring during the rainy season, and the October–November brood occurring during the dry season. Larvae were reared on individual plants

TABLE 1. Analysis of variance (ANOVA) for silk yield and related parameters in *Bombyx mori* as a function of genotype and environment. All parameters in the table are significant at $P < 0.01$.

Source	Mean sums of squares							
	Absolute silk yield	Fecundity	Larval weight	Larval span	E.R.R. %	Cocoon weight	Shell weight	Shell ratio
G (genotype)	9586.55	12288.29	28.20	9.30	248.93	17.24	0.28	3.76
E (environment)	83665.97	48260.00	353.27	105.02	737.35	174.57	22.62	533.27
G x E interaction	5663.00	5637.23	21.61	7.59	615.21	2.89	0.14	3.50

of *Terminalia arjuna* Bedd. (Combretaceae) situated in rows, with each plant separated by at least 2 m. Experimental design of the rearings followed a randomized block strategy during both generations, with three replicates of each genotype, 300 larvae per replication. Absolute silk yield was estimated based on shell weight of all the cocoons harvested from each replication. Gene-environment interaction was calculated following the methodology proposed by Plaisted and Peterson (1959). Analysis of variance (ANOVA) was calculated by pooling absolute silk yield of the two seasons.

Table 1 indicates that there were significant differences among genotypes (G), environments (E), and in the gene-environment interaction, suggesting that genotypes interact considerably with environmental conditions to produce different silk yields. Mean absolute silk yield for the two generations and within generation type variance (δ^2VL or stability) are illustrated in Table 2. Mean absolute silk yield ranged from 25.07 g to 147.78 g in the first generation, while that of the second generation ranged from 67.08 g to 259.73 g, illustrating a marked between generation difference. Absolute silk yield was found to be much higher in all genotypes during the second generation, corroborating the findings of Jolly et al. (1979).

As illustrated in Table 2, the genotypes in order of increasing absolute silk yield in the first generation were Palma (25.07 g), Laria (49.49 g), Sukinda (61.46 g), Raily (82.65 g), Nagri₁ (96.70 g), Sukli (98.98 g), Nagri₂ (100.64 g), and Nagri₃ (147.78 g). In the second generation, absolute silk yield (from least to greatest) was achieved by Laria, Nagri₃, Palma, Sukinda, Raily, Sukli, Nagri₂, and Nagri₁.

The estimate of genotype x generation variance exhibited a wide range from 792.96 to 4280.26 (Table 2). The greatest between-generation variability was demonstrated by Nagri₃ followed by Palma, Nagri₂, and Nagri₁. The least between-generation variability was demonstrated by Raily, followed by Sukli and Sukinda. These results suggest that greater stability in silk yield (between generations) could be obtained from Raily. Hence, this genotype would respond better to between-generation differences because of the lesser influence of environment on its absolute silk yield.

TABLE 2. Mean absolute silk yield and stability for eight genotypes of *Bombyx mori* reared in different environments.

Genotypes	Absolute silk yield in environment		G x E interaction
	Rainy season	Dry season	
Nagri ₁	96.70	259.73	2704.48
Nagri ₂	100.64	234.91	2819.07
Nagri ₃	147.78	123.63	4280.26
Sukli	96.98	181.01	952.31
Raily	82.65	157.58	792.96
Sukinda	61.46	156.66	991.73
Laria (P)	49.49	67.08	2190.97
Palma	25.07	148.01	3585.83

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DISTRIBUTION OF A NORTHERN FAUNA OF NOCTUIDAE IN THE MOUNTAINS OF OREGON

Additional key words: endemism, non-target species, biogeography.

Although the Oregon butterfly fauna has been well studied (Dornfeld 1980), comparatively little was known about the Oregon moth fauna until about 1960. During the past 30 years, extensive collecting has been conducted in the state, most notably by Stanley G. Jewett, Jr., C. William Nelson, James H. Baker, Elmer L. Griepentrog, Victor B. McHenry, Kenneth J. Goeden, and Jeffrey C. Miller. From 1992 through 1995, the U. S. Forest Service also conducted extensive blacklight (UV) trap sampling in the Cascade Range and the Blue Mountains to assess the impacts on nontarget Lepidoptera of *Bacillus thuringiensis* subsp. *kurstaki* sprays for suppression of outbreaks of western spruce budworm (*Choristoneura occidentalis* Freeman: Tortricidae) (see Grimble et al. 1992 for details of the sampling protocols in these studies).

Various components of this moth fauna show biogeographic connections with the northern Pacific Coast, California, the Great Basin, and the northern Rocky Mountains. In this paper, we report on a northern fauna of Noctuidae that is transcontinental across Canada from Quebec to British Columbia, extending southward through the Appalachians to North Carolina, the Rocky Mountains, and the mountains of Oregon. The fauna has been enumerated by Rockburne and Lafontaine (1976), Prentice (1962) and from a survey of museum records. Only those species typical of northern hardwood-conifer forests, meadows, or wetlands are included in this study; ubiquitous and/or migratory species throughout most of North America, such as *Heliothis zea* (Boddie) and *Peridroma saucia* (Hbn.), are excluded from consideration.

This northern noctuid fauna is largely confined to three mountainous regions of Oregon; the northern Coast Range, the Cascade Range, and the Blue Mountains. The northern Coast Range consists of low mountains 300–600 m in elevation, with a few higher peaks to 900 m, extending from Clatsop County to coastal Lane County. The Cascade Range extends from Multnomah and Wasco Counties south to Jackson and Klamath Counties. The lower Cascade foothills of the western slope extend from 150–1500 m, whereas the high Cascades are 1200–2100 m in elevation, with high volcanic peaks over 3000 m. The Blue Mountains extend from Crook County northeast to Wallowa County,

TABLE 1. Distribution of northern species of Noctuidae in the Coast Range (CO), Cascade Range (CA), and the Blue Mountains (BM) of Oregon. X = collected, O = not collected).

Species	CO	CA	BM
<i>Abrostola urentis</i> Gn.	X	X	O
<i>Acronicta fragilis</i> Gn.	X	X	X
<i>Acronicta funeralis</i> G.& R.	X	X	O
<i>Acronicta grisea</i> Wlk.	X	X	X
<i>Acronicta impleta</i> Wlk.	X	X	X
<i>Acronicta impressa</i> Wlk.	X	X	X
<i>Acronicta innotata</i> Gn.	O	O	X
<i>Acronicta lepusculina</i> Gn.	O	O	X
<i>Acronicta radcliffei</i> (Harv.)	X	X	O
<i>Agroperina inficita</i> (Wlk.)	O	O	X
<i>Agrotis obliqua</i> (Sm.)	O	X	X
<i>Agrotis venerabilis</i> Wlk.	O	X	X
<i>Aletia oxygala</i> (Grt.)	X	X	X
<i>Alypia langtoni</i> Couper	X	X	O
<i>Amphipoea americana</i> (Speyer)	X	X	O
<i>Amphipyra pyramidoides</i> Gn.	X	X	O
<i>Amphipyra tragopoginis</i> (Cl.)	X	X	X
<i>Anaplectoides prasina</i> D.& S.	X	X	X
<i>Anaplectoides pressus</i> (Grt.)	O	X	X
<i>Anathix puta</i> (G. & R.)	O	X	X
<i>Androloma maccullochi</i> (Kby.)	X	X	X
<i>Anhimella contrahens</i> (Wlk.)	O	X	X
<i>Apamea alia</i> (Gn.)	X	X	X
<i>Apamea amputatrix</i> (Fitch)	X	X	X
<i>Apamea finitima</i> Gn.	X	X	X
<i>Apamea impulsu</i> (Gn.)	X	O	O
<i>Apamea indocilis</i> (Wlk.)	X	X	X
<i>Apamea inordinata</i> (Morr.)	O	O	X
<i>Apamea lignicolora</i> (Gn.)	X	X	O
<i>Apamea plutonia</i> (Grt.)	X	O	O
<i>Apamea vultuosa</i> (Grt.)	X	X	X
<i>Aplectoides condita</i> (Gn.)	O	X	X
<i>Autographa ampla</i> (Wlk.)	X	X	X
<i>Autographa mappa</i> (G.& R.)	X	X	O
<i>Autographa pseudogamma</i> (Grt.)	O	X	X
<i>Autographa sansoni</i> Dod	X	X	O
<i>Brachylomia algens</i> (Grt.)	X	X	X
<i>Catabena lineolata</i> Wlk.	O	X	O
<i>Catocala briseis</i> Edw.	X	X	X
<i>Catocala relictata</i> Wlk.	X	X	X
<i>Catocala semirelictata</i> Grt.	X	X	X
<i>Chersotis juncta</i> (Grt.)	O	O	X
<i>Chortodes inquinata</i> (Gn.)	O	X	O
<i>Chortodes rufostrigata</i> (Pack.)	O	O	X
<i>Cosmia calami</i> (Harv.)	O	X	O
<i>Cucullia florea</i> Gn.	X	X	X
<i>Cucullia intermedia</i> Speyer	O	X	X
<i>Cucullia omissa</i> Dod	X	O	X
<i>Cucullia postera</i> Gn.	O	X	X
<i>Cucullia speyeri</i> Lint.	O	X	X
<i>Diachrysia aeroides</i> (Grt.)	X	X	X

TABLE 1. Continued.

Species	CO	CA	BM
<i>Diarsia rosaria</i> (Grt.)	X	X	X
<i>Egira dolosa</i> (Grt.)	O	X	X
<i>Enargia decolor</i> (Wlk.)	O	X	X
<i>Enargia infumata</i> (Grt.)	O	X	X
<i>Eosphropteryx thyatyroides</i> (Gn.)	X	X	X
<i>Eremobina claudens</i> (Wlk.)	O	X	X
<i>Eueretagtrotis perattenta</i> (Grt.)	O	O	X
<i>Euplexia benesimilis</i> McD.	X	X	X
<i>Eupsilia tristigmata</i> (Grt.)	X	X	X
<i>Eurois astricta</i> Morr.	O	X	X
<i>Eurois occulta</i> (L.)	O	X	X
<i>Eutricopis nexilis</i> (Morr.)	O	O	X
<i>Euxoa declarata</i> (Wlk.)	X	X	X
<i>Euxoa divergens</i> (Wlk.)	X	X	X
<i>Feralia comstocki</i> (Grt.)	X	X	X
<i>Galgula partita</i> Gn.	X	X	O
<i>Graphiphora haruspica</i> (Grt.)	X	X	X
<i>Hecatera sutrina</i> (Grt.)	O	X	O
<i>Heliothis phloxiphaga</i> G.& R.	X	X	X
<i>Helotrophia reniformis</i> (Grt.)	X	X	O
<i>Homorthodes furfurata</i> (Grt.)	O	X	X
<i>Hyppa xylinoides</i> (Gn.)	X	X	X
<i>Lacanobia grandis</i> (Gn.)	O	X	O
<i>Lacanobia lilacina</i> (Harv.)	X	X	X
<i>Lacanobia lutra</i> (Gn.)	X	X	X
<i>Lacanobia nevadae</i> (Grt.)	O	X	X
<i>Lacanobia radix</i> (Wlk.)	X	X	X
<i>Lacanobia subjuncta</i> (G.& R.)	X	X	X
<i>Lacanobia tacoma</i> (Stkr.)	X	X	O
<i>Lacinipolia olivacea</i> (Morr.)	X	X	X
<i>Lacinipolia vicina</i> (Grt.)	O	X	X
<i>Leucania insueta</i> Gn.	X	X	X
<i>Lithacodia albidula</i> (Gn.)	X	X	O
<i>Litholomia napaea</i> (Morr.)	X	X	X
<i>Lithomoia solidaginis</i> (Hbn.)	X	X	X
<i>Lithophane amanda</i> (Sm.)	X	X	X
<i>Lithophane baileyi</i> Grt.	O	X	O
<i>Lithophane georgii</i> Grt.	X	X	X
<i>Lithophane innominata</i> (Sm.)	X	X	X
<i>Lithophane petulca</i> Grt.	X	X	X
<i>Lithophane thaxteri</i> Grt.	O	X	X
<i>Luperina passer</i> (Gn.)	X	X	X
<i>Marathyssa inficita</i> (Wlk.)	O	X	X
<i>Melanchra adjuncta</i> (Gn.)	X	X	X
<i>Melanchra pulverulenta</i> (Sm.)	X	X	O
<i>Mniotype ducta</i> (Grt.)	O	X	X
<i>Mniotype tenera</i> (Sm.)	X	O	O
<i>Nephelodes minians</i> Gn.	O	O	X
<i>Nycteola cinereana</i> N.& D.	O	X	X
<i>Nycteola frigidana</i> (Wlk.)	X	X	O
<i>Ochropleura plecta</i> (L.)	X	X	O
<i>Oligia illocata</i> (Wlk.)	X	X	X
<i>Oncocnemis piffardi</i> (Wlk.)	O	X	O

TABLE 1. Continued.

Species	CO	CA	BM
<i>Oncocnemis riparia</i> Morr.	O	X	X
<i>Orthosia hibisci</i> (Gn.)	X	X	X
<i>Orthosia revicta</i> (Morr.)	X	X	X
<i>Orthosia segregata</i> (Sm.)	O	O	X
<i>Papestra cristifera</i> (Wlk.)	X	X	X
<i>Papestra quadrata</i> (Sm.)	O	O	X
<i>Paradiarsia littoralis</i> (Pack.)	O	O	X
<i>Phlogophora periculosa</i> Gn.	X	X	O
<i>Platyperigea meralis</i> (Morr.)	O	O	X
<i>Platypolia anceps</i> (Steph.)	O	X	O
<i>Polia nimbose</i> Gn.	X	X	O
<i>Polia purpurissata</i> (Grt.)	X	X	X
<i>Protolampra rufipectus</i> (Morr.)	X	X	X
<i>Proxenus miranda</i> (Grt.)	X	X	O
<i>Pyrria exprimens</i> (Wlk.)	X	X	X
<i>Raphia frater</i> Grt.	X	X	X
<i>Rhyacia quadrangula</i> (Zelt.)	O	X	X
<i>Scoliopteryx libatrix</i> (L.)	X	X	X
<i>Sideridis maryx</i> (Gn.)	O	X	X
<i>Sideridis rosea</i> (Harv.)	X	X	X
<i>Spaelotis clandestina</i> (Harr.)	O	O	X
<i>Stretchia plusiaeformis</i> Edw.	O	X	X
<i>Synedoida adumbrata</i> (Behr)	O	X	X
<i>Syngrapha alias</i> (Ottol.)	X	X	X
<i>Syngrapha epigaea</i> (Grt.)	X	X	X
<i>Syngrapha rectangula</i> (Kby.)	X	X	O
<i>Syngrapha viridisigma</i> (Grt.)	O	X	X
<i>Ufeus satyricus</i> Grt.	O	X	X
<i>Xanthia togata</i> (Esper)	X	X	O
<i>Xestia collaris</i> (G. & R.)	O	X	X
<i>Xestia smithii</i> (Snell.)	X	X	X
<i>Xylena cineritia</i> Grt.	O	X	X
<i>Xylena curvimacula</i> (Morr.)	O	X	X
<i>Xylena nupera</i> (Lint.)	X	X	X
<i>Xylena thoracica</i> (Putnam-Cramer)	O	X	X
<i>Xylotype acadia</i> B. & Benj.	X	X	X
<i>Zale duplicata</i> (Bethune)	O	O	X
<i>Zale lunata</i> (Drury)	X	X	X
<i>Zale minerea</i> (Gn.)	X	X	O

and include the Ochoco, Strawberry, Elkhorn, Wallowa and Imnaha Mountain ranges. Elevations are circa 1200–1800 m, with high peaks of 2700–3000 m. Both the Coast Range and the Cascade Range generally have a cool, moist climate due to the influence of the Pacific Ocean, although it is drier in the rain shadows on the eastern slopes. The Blue Mountains have a dry, more severe continental climate similar to the northern Rocky Mountains of Idaho and Montana.

To date a total of 143 of the 200 species of northern Noctuidae with a transcontinental distribution across Canada have been collected in the mountains of Oregon. Table 1 outlines the known distributions of these species in the Coast Range, Cascade Range, and the Blue Mountains. At present, we know of 707 species of Noctuidae recorded through-

TABLE 2. Number and percent of northern species of Noctuidae shared among the Coast Range (CO), Cascade Range (CA), and the Blue Mountains (BM) of Oregon.

Species	CO	CA	BM	CO/CA	CA/BM	CO/CA/BM
Number	4	8	15	22	34	60
Percent	3	6	10	15	24	42

out the state, and so these northern taxa comprise about 20% of the total Oregon fauna. Table 2 indicates the number and percent of northern species shared among the three mountain regions. For species restricted to a single region, the Blue Mountains have the highest number (15) and the Coast Range the fewest (4). However, the Cascade Range has the highest total number of northern species with 124, followed by the Blue Mountains with 109 and the Coast Range with 86.

This northern fauna is isolated and relictual in Oregon today, surviving on montane islands surrounded by broad expanses of desert lowlands and valleys. We postulate that these species dispersed southward into Oregon during the various glaciations of the Pleistocene. The modern distribution of endemically restricted species may suggest three dispersal routes into the state during the Pleistocene. These include a northeastern route into the Blue Mountains from the adjacent mountains of northern Idaho and Montana, a north-south route through the Cascades from British Columbia, and possibly some dispersal along the lower mountains of the Coast Range. Examples of such endemics include *Orthosia segregata* (Sm.), *Papestra quadrata* (Sm.), and *Zale duplicata* (Bethune) in the Blue Mountains; *Lacanobia grandis* (Gn.), *Oncocnemis piffardi* (Wlk.), and *Lithophane baileyi* Grt. in the Cascades; and *Mniotype tenera* (Sm.), *Apamea impulsiva* (Gn.), and *A. plutonia* (Grt.) in the Coast Range. Moreover, it is significant that a number of northern species known from the Washington Cascades do not cross the Columbia River valley into the Oregon Cascades. These include *Lithophane pexata* Grt., *L. fagina* Morr., *Anomogyna speciosa* (Hbn.), and *A. perquiritata* (Morr.).

In conclusion, about 71% of the northern transcontinental noctuid fauna are known to occur in the mountains of Oregon. It is doubtful that many additional species of this fauna remain to be discovered in Oregon, with perhaps the exception of the high Willowa Mountains where little survey work has yet been done.

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W. D. WINTER COLLECTION TO THE MUSEUM OF COMPARATIVE
ZOOLOGY, CAMBRIDGE

Additional key words: Geometridae, Noctuidae, New England.

In October 1996, the Lepidoptera collection of William D. (Dave) Winter (Westwood, Massachusetts) was donated to the Museum of Comparative Zoology at Harvard University (MCZ). This collection represents a most important regional taxonomic resource, with superbly prepared and documented specimens, often with an abundance of affiliated host-plant and related biological information. The Winter material at the MCZ presently totals 18,077 specimens, 16,079 from the 1996 donation and 1998 from donations between 1979–1989.

The strongest holdings are in the Noctuidae and Geometridae, although there is good representation of many groups. Virtually all the material was either collected personally by Dave, or reared by him from stock that he secured or obtained from other lepidopterists (few specimens are the result of direct exchange or gift). Dave ran a light trap for moths regularly in his back yard, with the back yard moving around in Westwood (from the early 1960s to 1975) and then on to nearby Dedham (1975 to 1995), in mostly semi-open environments with mixed hardwoods. Over time, the radius of his local butterfly and moth collecting expanded to include much of New England, Long Island, and northern New Jersey. Dave and his wife, Jo Brewer, also traveled extensively throughout North America to photograph and collect, with favored localities including Sanibel and Captiva Islands in Florida, and Ossibaw Island in Georgia.

Table 1 provides a synopsis of the MCZ donation. Several hundred specimens remain with Dave at present.

TABLE 1. Lepidoptera donated by William D. Winter to the Museum of Comparative Zoology at Harvard University.

Group	Year of Donation	
	1996	1979–1989
Hesperiidae	827	374
Papilionidae	436	33
Pieridae	256	135
Lycaenidae, Riodinidae	401	483
Nymphalidae	762	110
Satyridae	137	147
Danaidae	10	6
Pyrilidae	140	—
Thyatiridae, Drepanidae	92	—
Geometridae	3052	—
Mimallonidae, Apetalodidae, Lasiocampidae	94	—
Saturniidae	389	—
Sphingidae	296	—
Notodontidae	542	—
Arctiidae	786	—
Lymantriidae	87	—
Noctuidae	5443	810
mixed families	1408	—
exotics	837	—
unsorted microlepidoptera	827	—
	16079	1998

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MANUSCRIPT REVIEWERS, 1996

The merit of a scientific journal depends on the quality of its reviewers as well as its authors, but the former are usually unknown to readers. The *Journal* relied on the expertise of 61 reviewers last year to provide 108 evaluations of manuscripts. It is with much gratitude that the *Journal* acknowledges the services of the people listed below from whom manuscript reviews were received in 1996. Those who reviewed two or more manuscripts are denoted by asterisks.

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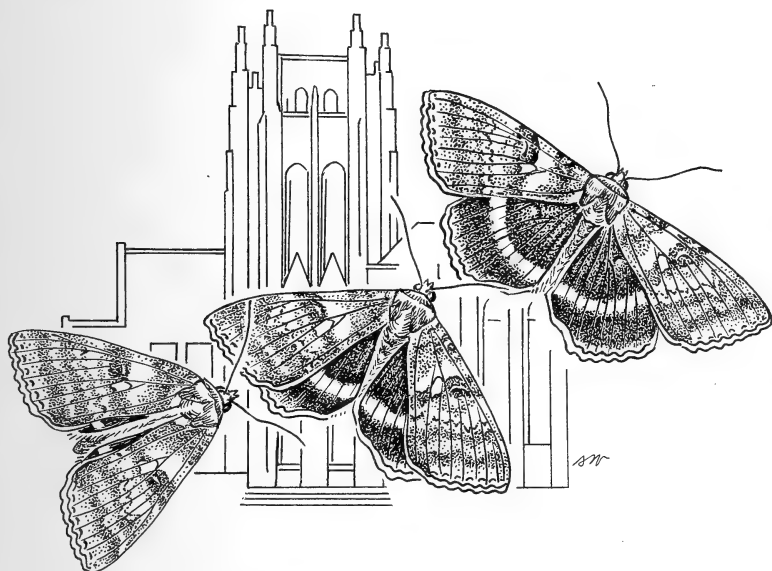
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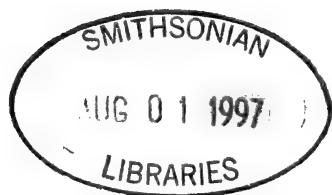
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THE IMMATURE STAGES OF *OXYTENIS MODESTIA*, WITH COMMENTS ON THE LARVAE OF *ASTHENIDIA* AND *HOMEOPTERYX* (SATURNIIDAE: OXYTENINAE)

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ABSTRACT. The immature stages of *Oxytenis modestia* are described, with special attention to the first instar, the larval food plants are reported, and larval and adult behaviors are described. Limited information is given for the genera *Homoeopteryx* and *Asthenidia*, and they are compared and contrasted with *Oxytenis*.

Additional key words: Life history, *Alibertia edulis*, *Genipa americana*, Rubiaceae.

The genus *Oxytenis* Hübner includes 17 described species of medium-sized moths (Jordan 1924) that are patterned to resemble dried, brown leaves (Fig. 1c). *Oxytenis* and two other genera, *Asthenidia* Westwood and *Homoeopteryx* Jordan, have been treated as the family Oxytenidae (Jordan 1924). Minet (1994) showed that these three genera do form a monophyletic group and, because he considered them to represent the most 'primitive' lineage of the Saturniidae, he reassigned them to that family as the subfamily Oxyteninae.

Unfortunately, technical descriptions for the larvae of Oxyteninae are still lacking. Brief, superficial descriptions are available for the larvae of some species: *Oxytenis naemia* Druce, *O. angulata* (Cramer), *O. ferruginea* Walker, *O. modestia* (Cramer) and *Asthenidia lactucina* (Cramer) (Jordan 1924, Draudt 1929). Nentwig (1985) described and illustrated

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the striking sequence of mimicry presented by various instars of *O. naemia*. Miles Moss produced a series of beautiful water color paintings of various oxytenine larvae, but these were never published and are in the Natural History Museum, London. Here we describe the immature stages and larval biology of *Oxytenis modestia*.

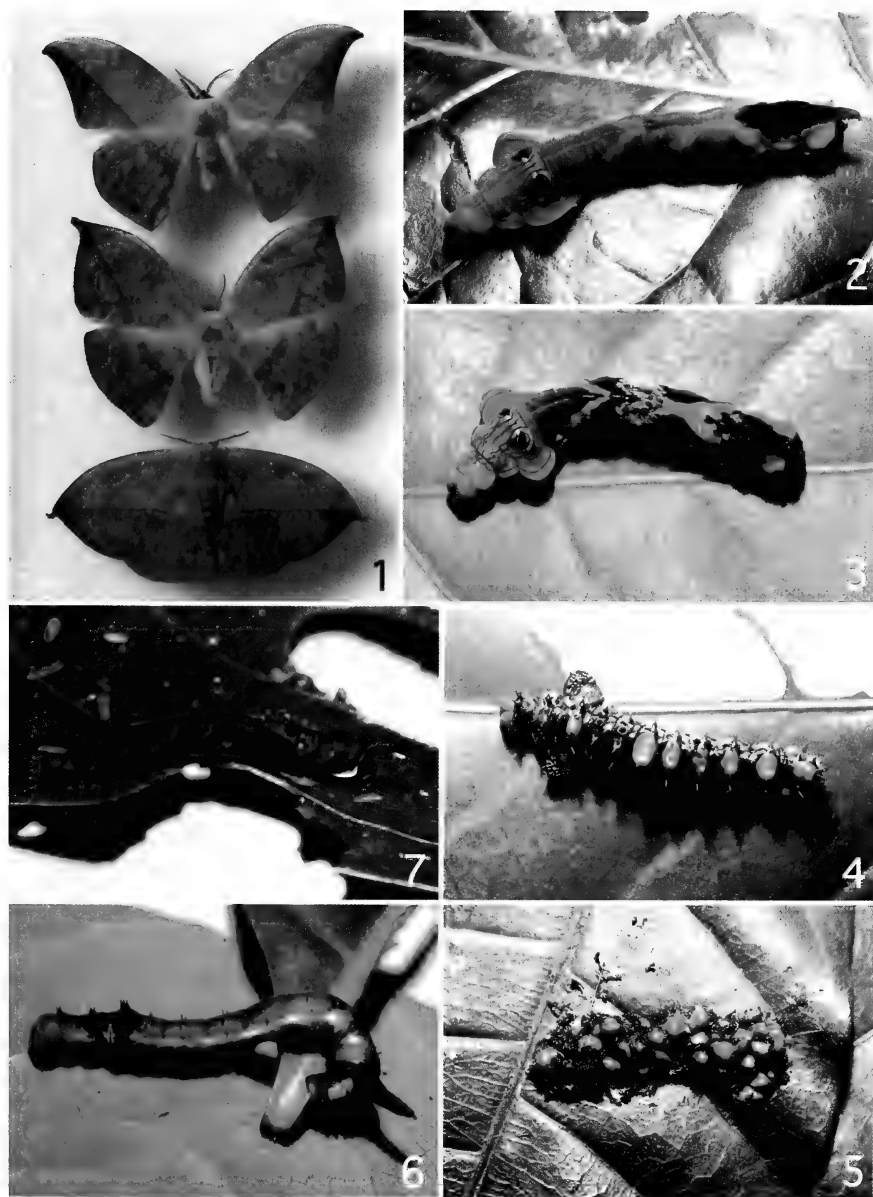
MATERIALS AND METHODS

Oxytenis modestia (Fig. 1) was reared by the senior author on several occasions, from larvae collected on *Alibertia edulis* (A. Rich.) A. Rich. and *Genipa americana* L. (Rubiaceae) (see Table 1 for list). The only eggs obtained (Aiello Lot 80-9) were from a female collected at light on Barro Colorado Island, Panama, on 8 March 1980.

Of the 96 eggs produced by the female, ten were preserved in 70% ethanol. The remaining 86 eggs were divided into four groups, placed in petri dishes, each with a piece of moist folded paper towel, and kept in ZipLoc bags in an air conditioned laboratory. Upon hatching, the larvae were offered squares of 11 different species of plants, all members of the Rubiaceae: *Alibertia edulis*, *Alseis blackiana* Hemsl., *Coussarea curvigemmia* Dwyer, *Faramea occidentalis* (L.) A. Rich., *Hamelia patens* Jacq., *Isertia haenkeana* DC., *Ixora coccinea* L., *Palicourea guianensis* Aubl., *Psychotria grandis* Sw., *Psychotria marginata* Sw., and *Randia armata* (Sw.) DC. The larvae preferred young leaves of *Alibertia* but ate small amounts of young *Alseis*, *Ixora*, and *Randia* as well. They were reared on *Alibertia edulis*. As they developed, the majority of the 86 individuals were preserved at various stages as vouchers, and only 12 individuals were reared to adults.

Specimens reared before 1981 are at the National Museum of Natural History (NMNH), Washington DC; those reared from 1981 to the present are at the Smithsonian Tropical Research Institute (STRI), Panama. Voucher specimens of all instars reared from eggs were preserved in 1:1 xylene:ethanol-95% (XA) and are at the NMNH. To study the morphology of the first instar in detail, two larvae were prepared for viewing in a Scanning Electron Microscope (SEM). The larvae were dehydrated in graded series of ethanol (70%, 80%, 90%, and 100%), then critical point dried in a DCP-1 Denton Vacuum with carbon dioxide. Specimens were then mounted on points and coated with a Denton Vacuum Desk II sputter coater, using a gold target, for 6 minutes (15 Ma). Prepared specimens were held on micro test clips (Radio Shack 270-373) and mounted on stubs for observation with a Hitachi 570s (15kV) SEM.

Morphological terms follow Dethier (1941) for the antennae, Grimes and Neunzig (1986a, 1986b) for the maxillae, Beck (1961) and Miller (1991) for tarsal setae, Stehr (1987) for chaetotaxy and general morphology, and Mosher (1916) for the pupae.



FIGS 1-7. **1-4**, *Oxytenis modestia*: **1 (upper)**: adult male (Aiello Lot 85-26), **1 (middle)**: adult female (Aiello Lot 81-65), **1 (lower)**: adult female (natural position) (Aiello Lot 84-55 no.4), 6.5 cm across; **2**, final instar (green morph) (Aiello Lot 80-9 no.1), 3.6 cm long; **3**, final instar (brown morph) (Aiello Lot 87-52 no.1); **4**, fourth instar (Aiello Lot 87-63), 2.6 cm long. **5**, bird-dropping, 2.1 cm long. **6**, *Homoeopteryx malecena* early final instar (Aiello Lot 79-122), 3.1 cm long. **7**, *Asthenidia transversaria* final instar (Aiello Lot 81-37), 3.5 cm long.

IMMATURE STAGES

Stock source. The female moth, collected as Aiello Lot 80-9, on 8 March, began ovipositing shortly after being placed in a wire and petri dish cage with a leaf of *Faramea occidentalis*. Before dying on 12 March, she laid 96 eggs on the floor paper and the wire walls, as well as on the leaf.

Egg. Duration 5 days. Ellipsoid, approximately 1.3 mm in length, green. The eggs were green when fresh, but gradually faded to yellow by day five. By day three, the stemmata began to show through the chorion of some individuals, and by day four the mandibles were visible. On day five, the final day of the egg stage, the larvae could be seen clearly. They were folded twice to form a condensed 'S,' and they slowly shifted position within the egg.

First instar, general. Duration 4–5 days. Pale beige in color; head 0.6 mm wide; body 3.8–4.2 mm long; primary setae represented by granulate setae and chalazae with bulbous glandular tips that secrete a sticky substance. **Head:** (Figs 8, 9), hypognathous; surface smooth with long primary setae and without secondary setae, F1 very short, C2 arises from the lateral margin of the clypeus and runs parallel to the head surface, A1 shortest A seta, S2 and A3 well above the stemmatal semicircle; stemmata 1–2 and 3–4 very close forming a semicircle, stemma 5 distant and ventral to 6; ecdysial line and fronto-clypeal suture inconspicuous; adfrontal suture conspicuous only for upper half of the frons; anteclypeus grooved; labrum with six pairs of setae, without notch; mandibles quadrate with five opposable teeth; antennae (Fig. 11) prominent, segment 1 short; segment 2 with two sensilla trichodea (ST) on the external side, sensillum anterior several times larger than caudal sensillum, with three sensilla basiconica (SB), the larger ones near the anterior and posterior margins of the segment, the small SB half-way between the anterior SB and ST; segment 3 projecting, located medially with respect to S2; sensillum styloconicum (SC) as long as longest sensillum basiconicum, and located in the posterior and anterior margins respectively, two small SB medially and laterally; maxillary lobe with STI removed ventrolaterally from and larger than STII–III, all acicular; MSS and LSS subequal; all other sensilla inconspicuous; maxillary palpus with all eight sensilla basiconica subequal; spinneret (Fig. 12) dorsoventrally compressed, truncate. **Thorax:** relatively smooth; spiracle oval, as large as that on A7; primary setae XD, D and SD represented by chalazae with setae bearing bulbous glandular tips (Figs. 9, 10, 16), except for D1 and D2 on T1 and D2 on T2, which are thick setae; L group with two setae on T1, and one on T2–3; two SV and one V on all three segments; thoracic legs with seta 2 (Ts2) acicular (Fig. 13), Ts3 and Ts1 lanceolate, Ts3 slightly longer than Ts1. **Abdomen:** A1–8 with D1 and SD1 as chalazae with gland-tipped setae, only one SD, L, and SV setae; a minute, round spiracle on A1–6, A7 with an oval larger spiracle, A8 with largest, circular spiracle; a chalaza with gland-tipped seta as D1 on anal shield. Crochets 6 or 7, in a uniordinal homoideous mesoseries plus 4–5 crochet remnants of a uniordinal lateroseries. Crochets not deeply set in the spatula on the proleg; the fleshy lobe of the proleg gives the crochets a more or less C-shaped pattern (Fig. 15). The first instars emerged from their eggs the morning of day six and, after testing them with a variety of rubiaceus plants, all were reared on *Alibertia edulis*.

Second instar. Duration 3–5 days. Similar to first instar except that the chalazae are larger and are drawn out to form a stalk, tipped by a sticky gland; the metathoracic, L chalaza is located on a tiny triangular lateral flange and is gland-tipped; the D1 chalazae of A8 are located at the tip of a fleshy 'tail,' and the larva is now darker and has the overall appearance of a bird dropping.

Third instar. Duration 4–6 days. A larger version of the second instar, except that it is black with large brown chalazae (Fig. 4) and is an excellent mimic of a bird dropping filled with seeds (Fig. 5).

Fourth instar. Duration 3–5 days. Essentially the same as the third, only larger.

Fifth instar. Duration 6–7 days if final, 3–4 days if not final. This species has a variable number of stadia, independent of sex, and the final instar is different from the others, whether instar 5 or 6. If the fifth instar is not the final instar, it looks essentially the same as the three previous instars, only larger. If the fifth instar is the final instar, it takes on a different appearance, a description of which appears under "sixth instar."

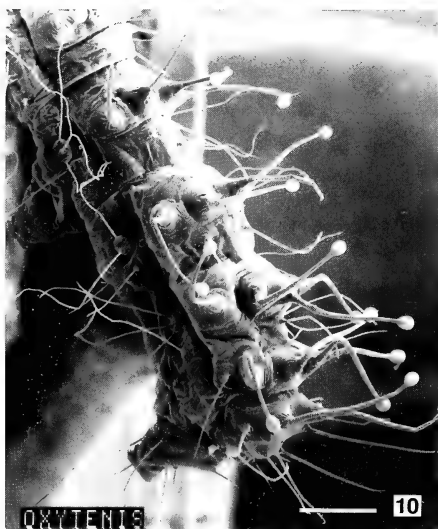
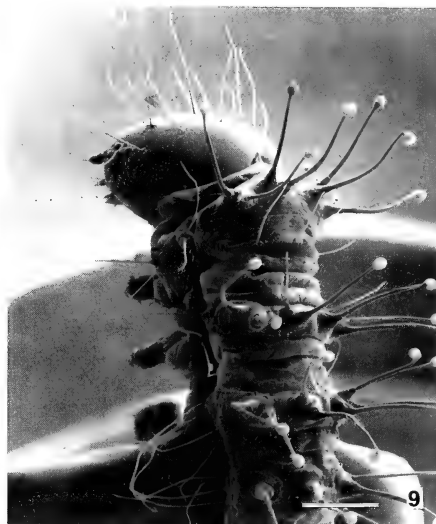
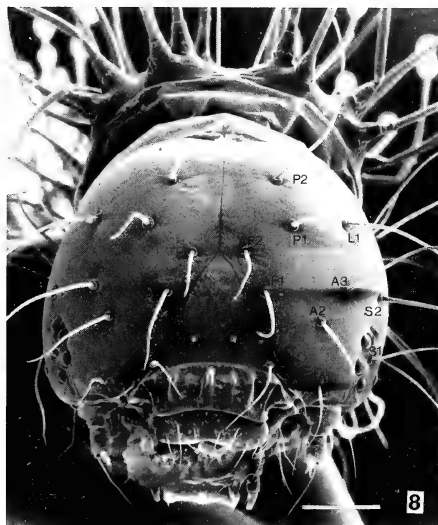
TABLE 1. *Oxytenis modestia*, *Homoeopteryx macelena*, and *Asthenidia transversaria* reared by the senior author.

Stage collected	Number adults obtained	Larval food plant (Rubiaceae)	Aiello lot #
<i>Oxytenis modestia</i>			
Eggs	7 m, 5 f		80-9
Third to final instar	1 f	<i>Genipa americana</i> L.	84-55
Second to final instar	1 m	<i>Genipa americana</i> L.	85-126
Penultimate instar	1 m	<i>Alibertia edulis</i> (A. Rich.) A. Rich. in DC.	81-43
Penultimate instar	1 f	<i>Alibertia edulis</i> (A. Rich.) A. Rich. in DC.	81-65
Penultimate instar	1 m	<i>Genipa americana</i> L.	87-52
Final instar	1 f	<i>Alibertia edulis</i> (A. Rich.) A. Rich. in DC.	80-46
Final instar	1 f	<i>Genipa americana</i> L.	78-90
Pupa	1 f	<i>Genipa americana</i> L.	78-91
<i>Homoeopteryx malecena</i>			
Penultimate instar	1 f	<i>Fareamea occidentalis</i> (L.) A. Rich.	82-24
Second to final instar	1 f	<i>Fareamea occidentalis</i> (L.) A. Rich.	82-49
Third to final instar	1 m	<i>Fareamea occidentalis</i> (L.) A. Rich.	82-78
Penultimate instar	1 f	<i>Fareamea occidentalis</i> (L.) A. Rich.	79-122
Final instar	1 f	<i>Fareamea occidentalis</i> (L.) A. Rich.	80-74
<i>Asthenidia transversaria</i>			
Final instar	1 f	<i>Calycophyllum candidissimum</i> (Vahl) DC.	81-37
Penultimate instar	1 m	<i>Warscewiczia coccinea</i> (Vahl) Kl.	81-67

Sixth instar: Duration 6–8 days. Regardless of whether it is the fifth or the sixth, the final instar looks quite different from any of the preceding instars and it occurs as either a green or a brown morph, with variations. In all cases, the metathorax bears subdorsal eye spots (black, bordered by yellow) towards the anterior margin. These ‘eyes’ are located in a fold of cuticle and thus can be ‘opened’ and ‘closed’ by raising or lowering blood pressure to the thorax. At rest the eyes are closed, but a highly disturbed larva inflates the thorax, thus opening the ‘eyes,’ and rears up, waving back and forth like an angry serpent. In this stadium, the glands are tiny and sessile on the body, and the L gland of the metathorax is missing. The green morph (Fig. 2) is dark green with a bright green dorsal stripe that widens on A4, narrows on A5, then widens again to cover the sides of the body on A6–8. A long black dorsal diamond mark on A6–8 terminates with the ‘tail.’ Occasional individuals have the dorsal stripe cryptically marked with brown, yellow, green, and black. Brown individuals (Fig. 3) are like the green ones except that the ground color and dorsal stripe are brown; the head remains green, however.

Larvae, general: Individuals passed through five to six larval instars (Table 2). Larval stadia were trimorphic, that is the general appearance of each larva changed abruptly upon the molt to second instar and changed again upon molting to the final instar, regardless of whether that final instar was the fifth or the sixth. The condition of trimorphic larval stadia together with a variable number of larval instars occurs as well in the nymphalid *Dynastor darius* (Fabricius) (Aiello, 1978), and in the saturniid *Arsenura batesii* (Aiello, pers. obs.). In the case of *Oxytenis* the situation is more complex because, in addition, the larvae are polymorphic for color pattern within the later intermediate stadia and the final stadium; some individuals are green (Fig. 2) and some are brown (Fig. 3), regardless of sex, and they show varying degrees of pattern complexity. As the result of this variation in color and development the larger larvae of a brood tend not to resemble one another; the multiple search images resulting from such variation perhaps make them less easy for a predator to locate.

From the outset, the larvae assumed a ‘J’ position, with the head and thorax turned back



FIGS. 8-11. **8**, *Oxytenis modestia* first instar, head (front view) (Aiello Lot 80-9). A = anterior setae, AF = adfrontal setae, C = clypeal setae, F = frontal setae, L = lateral setae, P = posteriodorsal setae, S = stemmatal setae. Scale line = 0.15 mm; **9**, *Oxytenis modestia* first instar, head and thorax (lateral view) (Aiello Lot 80-9). Scale line = 0.3 mm; **10**, *Oxytenis modestia* first instar, abdominal segments 6-10 (lateral view) (Aiello Lot 80-9). Scale line = 0.25 mm; **11**, *Oxytenis modestia* first instar, right antenna (ventral view, with anterior at top) (Aiello Lot 80-9). Scale line = 11.55 μ m.

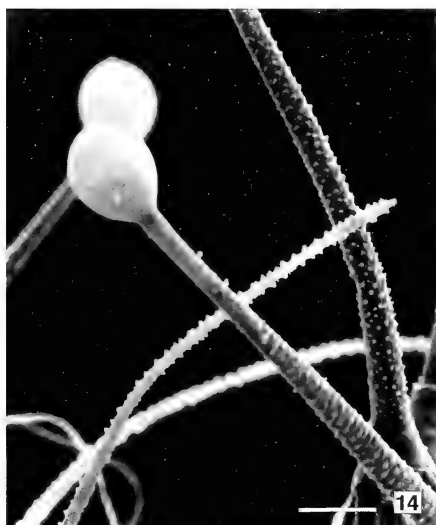
to one side and pressed against the abdomen when mildly disturbed or when at rest, a behavior that continued throughout larval life, and which, especially in the intermediate instars, gave the larva the appearance of a bird dropping. All larval instars bore sticky glands. Perhaps to avoid contamination of these glands, the larvae grasped their fecal pellets in



12



13



14



15

FIGS. 12–15. **12**, *Oxytenis modestia* first instar, hypopharyngeal complex (dorsal view with anterior at top). (Aiello Lot 80-9). Scale line = 37.5 μ m; **13**, *Oxytenis modestia* first instar, right pretarsus of mesothoracic leg (mesal view) (Aiello Lot 80-9). Scale line = 25 μ m; **14**, *Oxytenis modestia* first instar, gland-tipped setae (D on A2–3, detail) (Aiello Lot 80-9). Scale line = 37.5 μ m; **15**, *Oxytenis modestia* first instar, left proleg (Aiello Lot 80-9). Scale line = 25 μ m.

their mandibles as they were produced and dropped them off the leaf. Interestingly, the earliest instars of various *Oxytenis* species are superficially similar, in color and pattern, to the earliest instars of various species of *Adelpha* Hübner (Nymphalidae) that feed on the same array of rubiaceous plants (Aiello, pers. obs.). The larvae remained on the upper surface of their food leaves except during molting, at which time they moved to the wall of

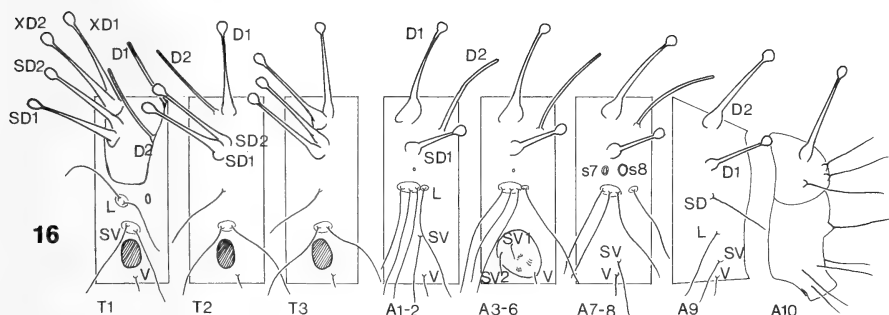


FIG. 16. *Oxytenis modestia* first instar, setal map. A = abdominal segment, D = dorsal setae, L = lateral setae, s = spiracle, SD = subdorsal setae, SV = subventral setae, V = ventral seta, XD = extradorsal setae.

the petri dish. In the wild, larvae of *Oxytenis modestia* usually move to the petioles and branches to molt, although they may remain on the blade (Aiello, pers. obs.).

Pre-pupa: Much faded and shortened, with the 'eyes' opened. Mature larvae constructed very loose cocoons of leaves and wet, stretchy, reddish silk on the floor of the cage, and they produced a copious puddle of liquid in which the pre-pupae rested. Being shrunk, faded, and wet, they appeared dead and rotten, but, the next morning, they pupated. The production of liquid by pre-pupae has been reported for two sphingids, *Manduca* (as *Protoparce*) *rustica* (Fabricius) (Moss 1912) and *Xylophanes mossi* Clark (Moss 1920).

Cocoon: Very loose cocoon of leaves and wet, stretchy, reddish silk.

Pupa (Fig. 17a shows *Oxytenis naemia*): Duration 12–14 days. Obtect; fronto-clypeal suture obsolete; labial palpi not visible; pilifer lobes absent; the maxillae and prothoracic legs the only appendages visible within the area delineated by the antennae; antennae broadly pectinate, touching for the apical 0.5–2 mm, the width one seventh the length; mesothoracic wings, on the ventral surface of the body at meson, shorter than caudal margin of the fourth abdominal segment; abdominal segments with scattered minute setae not visible without magnification; cremaster with approximately 24 reddish hooks, which are quite tangled together.

Larval food plants: *Alibertia edulis* and *Genipa americana* (Rubiaceae).

Adults. Adults eclosed around 11 pm and the females began emitting pheromone about 2.5 hours later. The resemblance of the adults to dried, brown leaves is greatly enhanced by the behavior of the moths, which rest with the wings held so as to form a 'leaf,' complete with midrib, petiole, and drip tip. When disturbed, the moths release their grip on the substrate and gently waft to the ground.

Distribution and flight period. Guatemala to Bolivia and southeastern Brazil, presumably occurring also in Mexico and northern Argentina; flying during March to December (Jordan, 1924). On Barro Colorado Island, adults can be seen at any time of year, although they are rare from November through April, and are most abundant from May through July.

NOTES ON HOMEOPTERYX AND ASTHENIDIA

Homoeopteryx malecena Druce has been reared by the senior author on three occasions from larvae found on *Faramea occidentalis*, and *Asthenidia transversaria* Druce has been reared twice from larvae, once on *Calycophyllum candidissimum* (Vahl) DC. and once on *Warscewiczia coccinea* (Vahl) Kl. (Table 1). All three plants belong to the Rubiaceae.

TABLE 3. Distribution of sticky glands for *Homoeopteryx*, *Asthenidia*, and *Oxytenis*. Values in table are total number of sticky glands per segment, for thoracic segment 1 through abdominal segment 10.

		T1	T2	T3	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10
<i>Homoeopteryx</i>	early instars	8	8	8	4	4	4	4	4	4	4	4	4	2
	final instar	8	10	10	6	6	6	6	6	6	6	6	6	6
<i>Asthenidia</i>	final instar	8	6	10	4	4	4	4	4	4	4	4	6	2
<i>Oxytenis</i>	early instars	8	6	8	4	4	4	4	4	4	4	4	4	2
	final instar	8	6	10	4	4	4	4	4	4	4	4	4	2

***Homoeopteryx*.** Although adults of *Homoeopteryx* are superficially very similar to those of *Oxytenis* in general appearance, the larvae of the two genera differ in several respects. Although all instars we have seen bear sticky glands and rest in a 'J' position, they lack the flanges and eye-spots of *Oxytenis*, and the gland pattern of *Homoeopteryx* appears to be more complete than that of *Oxytenis* (Table 3).

The youngest larva seen (Aiello Lot 82-78), was cream colored along the dorsum and purple-brown along the sides. Its sticky glands were at the ends of long setae and were distributed as shown in Table 3 for early instars. The head had long white setae, without glands, and glandless setae were also found among the gland-tipped ones. The distribution of setae with glands was the same as for early instar *Oxytenis* except that *Oxytenis* had only 6 gland-tipped setae on T2, whereas *Homoeopteryx* had 8. Judging by the long, gland-tipped setae, it is most probable that this early larva was a first instar, and if so, then that individual had only four larval instars.

The next instar was cream, cryptically patterned with black, and had a poorly-defined cream saddle on segments A4–A6. The glands were sessile on slender chalazae instead of at the tips of setae. The chalazae of T3 were located on an annular swelling, which could be folded forward against the body. The D chalazae (with sticky glands) of A8 were at the apex of a short 'tail' giving that protuberance a slightly forked appearance. The gland pattern changed (Table 3) in that T2 and T3 now had 10 instead of 8 glands, and the abdominal segments now each had 6 glands instead of 4.

The following instar was a larger, paler version of the previous one, except that the T3 swelling was more pronounced and the 'tail' was rather thick.

The final instar was at first quite dark, although the cream saddle was still visible. As the larva matured, it became less dark, more evenly cryptically marked, and the saddle mark darkened somewhat. In general, the larva became an excellent twig mimic, a resemblance that was greatly enhanced by the T3 annular swelling, the slightly paler saddle mark, and

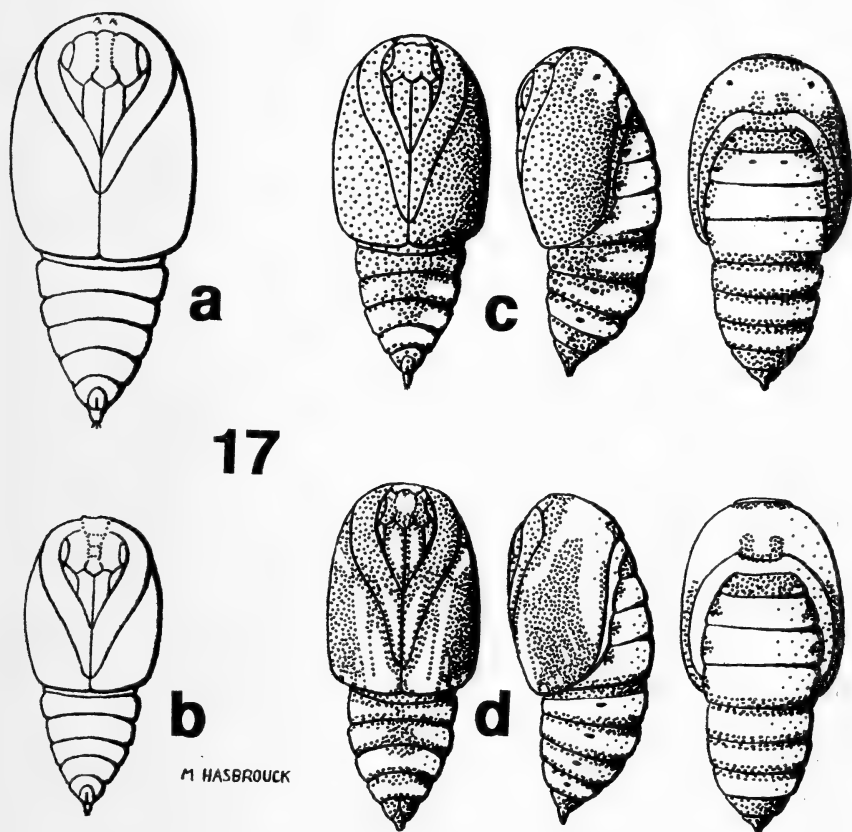


FIG. 17. Pupae. **a**, *Oxytenis naemia*, ventral view (Lot 81-80 no.4), 2.4 cm long; **b**, *Asthenidia transversaria*, ventral view (Lot 82-67), 1.4 cm long; **c-d**, *Homoeopteryx malecena*, ventral, lateral, and dorsal views (c: Lot 82-78, d: Lot 82-24), each 2.2 cm long.

the fact that the larva rested with the body held rigid with the anterior end held up at a slight angle, in the manner of many geometrids.

Among other individuals reared, the intermediate instars were gray and cryptically marked with a green and brown lichen-like pattern. Mature larvae may also be cryptically marked or may be the same mossy green of their food plant leaves (Fig. 6).

The larva made a leaf and silk cocoon in which it pupated several days later. The pupa (Fig. 17c,d), instead of the uniform dark brown to black of an *Oxytenis* was dark beige with black markings, and the pattern varied among individuals.

***Asthenidia*.** Adults of *Asthenidia* bear no resemblance to either *Oxytenis* or *Homoeopteryx*, and instead look like small, white swallow-tail butterflies. However, the 'tail' and eyespots of the mature larva

(Fig. 7) reveal it to be an oxytenid. The larva reared on *Calycophyllum candidissimum*, was nearly mature when collected and the one reared on *Warscewiczia coccinea* was collected the day before it molted to the larval final stadium. Both larvae rested in a 'J' position on the upper surface of leaves.

The younger of the two larvae bore stalked glands with non-glandular setae at the bases. The glands were arranged as in the early instars of *Homoeopteryx*. There were false eyes on T3 that could open and close as in *Oxytenis*. Although there were no thoracic flanges, the metathorax (T3) was slightly expanded and each expansion bore a single gland. As well, there were two humps, each with two peaks, one on T3 and one on A3. The 'tail' on A8 had two glands at the apex and had an extra point posterior to and below the apex. The larva was cryptically patterned with gray, brown and whitish, and had a low lateral white area on A3-4 and A7-8.

The final instar had deep blue eye spots with a broad black border. The thorax expansions were now almost non-existent. The hump on T3 was high and had two peaks close together. A3 had two large bumps. The tail had a posterior bump at the mid point. The larva was very dark green to black, except dorsally from the posterior side of the T3 hump, narrowing between the A3 humps, to a small dorsal green triangle on A4, then widening on A5 to a broad green dorsal stripe that swept up and included the 'tail.' There was a subventral white mark on each of A4 and A7-8. Many glands were missing and the few remaining glands were sessile and were best formed on segments T1-A8.

The other final instar was similar but was brown instead of green, and the black was confined to the subventral areas and to bold oblique lateral marks on A3, A4, small lateral triangles on A6 and A7, and a dark lateral crescent on A4-6. It also had a subventral white mark on A7-8. The only definite glands were on the prothorax, in two groups of four, and they were sessile.

Both larvae made loose cocoons of leaf and silk. The pupae (Fig. 17b) were short compared with those of *Oxytenis*, and the abdomen came to a more acute point.

SYSTEMATIC RELATIONSHIPS

The possession of sticky glands by the larvae, the habit of resting in a 'J' position, the utilization of rubiaceous food plants, and the similarities of pupal morphology seem to tie the three genera, *Homoeopteryx*, *Asthenidia*, and *Oxytenis* together. The distribution of sticky glands is similar for the three genera in the early stadia. In later stadia, the distribution is more complete for *Homoeopteryx* than for *Oxytenis* or *Asthenidia* (Table 3). That, plus the fact that *Homoeopteryx* has no tho-

racic flanges or eye spots leads us to believe that that genus is more generalized and nearer to the ancestral condition than are the other two. *Asthenidia*, with its eye spots and thoracic expansions is more reminiscent of *Oxytenis*. Based upon a handful of rearings, *Homoeopteryx* and *Asthenidia* may each be confined to a more limited selection of larval food plant, while the various species of *Oxytenis* are found on plants of at least five genera, *Alibertia*, *Faramea*, *Genipa*, *Isertia*, and *Posoqueria*.

Both Jordan (1924) and Michener (1952) indicated that the use of larval characters, especially from the first instars, in Oxyteninae and Cercophaninae could be of great help in understanding phylogenetic relationships among Saturniidae. Nevertheless, the known larvae of *Oxytenis* show many specialized characters, such as the sticky scoli, that make it very difficult to determine character homology. A similar situation was found for *Cercophana venusta* (Walker) (Wolfe & Balcázar 1994). Nässig (1989) proposed a classification of the scoli found in the Saturniidae (not including the Oxytenidae), but the peculiar type found in the Oxyteninae does not conform to any proposed classification. Interestingly, Oxyteninae and Cercophaninae, the two most plesiomorphic subfamilies in Minet's classification, have the D scoli on A8 not fused on the dorsomeson, the most characteristic feature of the bombycoid larvae that have few secondary hairs ("naked") (Lampe & Nässig 1989, Nässig 1994, Oberprieler & Duke 1994). Fused D scoli on A8 was regarded as a synapomorphy for the Bombycoidea by Minet (1994), under the assumption that its absence in some taxa (bombycoid larvae clothed in long secondary hairs, "wooly," and the "naked" larvae of *Salassa* Moore [Salassinae], *Anisota* Hübner, and *Dryocampa* Harris [Cerato-campinae]) is the result of secondary loss. It remains to be resolved whether these structures are synapomorphic or the result of convergence reflecting the same groundplan (cf. Oberprieler & Duke 1994).

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A NEW SPECIES OF *PHANETA*, WITH TAXONOMIC
DIAGNOSES AND SEASONAL AND GEOGRAPHICAL DATA
ON FOUR RELATED SPECIES (TORTRICIDAE)

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ABSTRACT. *Phaneta canusana*, new species, is described and compared with *P. lapidana*, *P. sublapidana*, *P. kokana* and *P. ambodaidaleia*. Lectotypes are designated for *P. lapidana* and *P. sublapidana*. Imagos of the five species, the male genitalia of *P. lapidana* and *P. sublapidana* and the male and female genitalia of *P. canusana* are illustrated. *P. canusana* is associated with prairie remnants in Ohio, Kentucky, Missouri, and Mississippi. New distribution records are given for *P. kokana* and *P. ambodaidaleia*.

Additional key words: vernal flight, autumnal flight.

The genus *Phaneta* Stephens consists of 102 species in North America, including eight described since publication of the most recent check list for North American members of the genus (Powell 1983). This group was treated by Heinrich (1923) as *Thiodia*, distinguishable from *Eucosma* by the absence of a costal fold on the male forewing. Obraztsov (1952) restricted *Thiodia* to a group of European species and considered *Phaneta* to be the correct generic name for the Nearctic species.

While surveying the lepidopteran fauna of Lynx Prairie Preserve, Adams County, Ohio, in 1989 and the Osborn prairie remnant of the Mississippi Black Belt in 1991, we recorded an unknown species of *Phaneta*, described below as new. Representatives of this same species had been collected in Missouri by J. Richard Heitzman in 1976, and they were brought to our attention by W. E. Miller, who recognized the conspecificity of the Missouri and Ohio specimens. The new species has similarities with four other members of the genus: *P. lapidana* (Walsingham), *P. sublapidana* (Walsingham), *P. kokana* (Kearfott), and *P. ambodaidaleia* Miller.

In examining olethreutine type specimens residing in European collections, Obraztsov selected specimens to serve as lectotypes for Walsingham's species, but he never published those designations. His notes and photographs of this material are currently on loan to the Mississippi

Entomological Museum from the American Museum of Natural History (AMNH), and based on that information, lectotypes are designated in this paper for *P. lapidana* and *P. sublapidana*.

During this study, specimens from the following institutional and personal collections were examined: Horatio T. Enterline (HTE), Loran D. Gibson (LDG), J. Richard Heitzman (JRH), Illinois Natural History Survey (INHS), Mississippi Entomological Museum (MEM), United States National Museum of Natural History (USNM), Donald J. Wright (DJW), and Zoological Museum, Copenhagen (ZM).

Phaneta sublapidana (Walsingham)

(Figs. 1, 2)

Semasia sublapidana, Walsingham 1879:59, pl. 73, fig. 9 (imago)

Thiodia sublapidana, Fernald [1903]:462; Heinrich 1923:50, fig. 122 (male genitalia); McDunnough 1939:44.

Eucosma sublapidana, Barnes & McDunnough 1917:no. 7086.

Phaneta sublapidana, Powell 1983:33.

Semasia sublapidana was described from four males collected near Klamath Lake, Oregon. A **lectotype** for *Semasia sublapidana* Walsingham is hereby designated (Fig. 1): male, "(nr. Fort Klamath), Jackson Co., Oregon, 21–23 IX 1871, Wlsm." BM genitalia slide 11599 (Fig. 2). The lectotype is deposited in The Natural History Museum, London (BMNH). According to Obraztsov's notes on the envelope containing the photograph of the lectotype, this was the specimen figured by Walsingham (1879).

We examined the following specimens: California: Mono Co., NE side Mono Lake, 6500', XI-19-93, D. Giuliana, 1400 PST [Pacific Standard Time], 46° F (1). Inyo Co., Deep Spr. Vy., 5300', XI-23-93, D. Giuliana, 1600 PST, 36° F (1) (UCB). J. Powell (pers. comm.) collected a series of 18 males during the second week of December, 1995 in the Owens Valley, Inyo County. These individuals were flying just before sunset, which occurs at 1600 h in December in the eastern shadow of the Sierra Nevada Mountains.

Phaneta lapidana (Walsingham)

(Figs. 3, 4)

Semasia lapidana, Walsingham 1879:58, pl. 73, fig. 8 (imago)

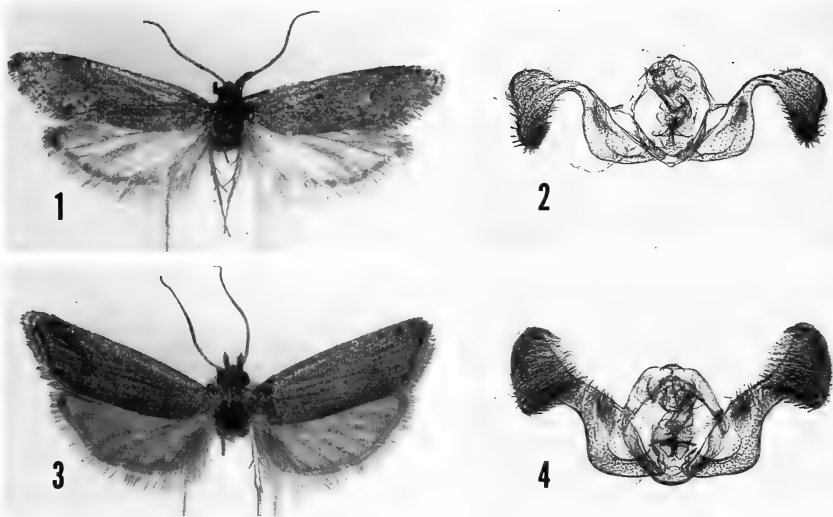
Thiodia lapidana, Fernald [1903]:462; Heinrich 1923: 50; McDunnough 1939:44.

Eucosma lapidana, Barnes & McDunnough 1917:no. 7085.

Thiodia lapidana, Heinrich 1929:2, fig. 7 (male genitalia) [missp.].

Phaneta lapidana, Powell 1983:33.

The description of *Semasia lapidana* was based on one male and two females collected at Crooked River near Klamath Lake, Oregon on September 22, 1871. A **lectotype** for *Semasia lapidana* Walsingham is hereby designated (Fig. 3): male, "Crooked R. (nr. Fort Klamath) Jackson Co., Oregon, 21–23 IX 1871, Wlsm." BM genitalia slide 11598 (Fig. 4). The lectotype is deposited in BMNH. According to Obraztsov's notes on the envelope containing the photograph of the female cotype of *S. lapidana*, the detached abdomen accompanying this specimen is that of a male. Obraztsov's photograph of this male genitalia reveals that it belongs to a specimen of *Epinotia columbia* (Kearfott), which has been treated historically as a junior synonym of the Palearctic species, *E. crenana* (Hübner). The latter was also collected by Walsingham at Crooked River and misidentified as a smaller form of *Epinotia* (sensu *Proteopteryx*) *emarginana* (Walsingham) (1879: pg. 69). We examined the following specimen: British Columbia: Chilcotin, 15-IX-1925, George V. Copley.



FIGS. 1-4. Lectotypes of *Phaneta* species described by Walsingham from Jackson County, Oregon. 1, *P. sublapidana*, male imago; 2, *P. sublapidana*, male genitalia, B.M. slide 11599; 3, *P. lapidana*, male imago; 4, *P. lapidana*, male genitalia, B.M. slide 11598.

Phaneta kokana (Kearfott)
(Fig. 5)

Eucosma kokana, Kearfott 1907:29.

Eucosma chortaea, Meyrick 1912:35 [invalid repl. name].

Hystricophora kokana, Heinrich 1923:259 (lectotype designation).

Thiodia sororiana, Heinrich 1923:263, fig. 421 (male genitalia); McDunnough 1939:44 (as subspecies of *Thiodia kokana*).

Thiodia kokana, Heinrich 1924:387; McDunnough 1939:44.

Phaneta kokana, Powell 1983:33; Godfrey et al. 1987:35.

Eucosma kokana was based on a female from Cincinnati, Ohio and a male from Scranton, Pennsylvania. Heinrich (1923) designated the female as lectotype and placed the species provisionally in *Hystricophora*. In the appendix to that same paper, Heinrich described *Thiodia sororiana* and figured the male genitalia based on specimens from Aweme, Manitoba, noting that he had seen specimens of the same species from Ontario, Canada in the Fernald Collection. He stated that the forewing had a dark band bordering the termen, differentiating it from *P. lapidana*, and that it most closely resembled *Hystricophora kokana* (Kearfott), based on examination of a female specimen of the latter. Following receipt of additional specimens of *P. kokana* from Cincinnati, Heinrich (1924) synonymized *T. sororiana* with *E. kokana* and transferred *kokana* to *Thiodia*. To confirm the identity of our specimens, a photograph of a female was compared with the lectotype of *P. kokana* in the AMNH.

In *P. kokana* the forewing is divided roughly into a dark basal area and pale apical area, the latter extending from beyond the middle of the costa across the wing to the tornus and outward to the apex. The basal area bears a mixture of light brown scales, gray scales, and gray scales with white or black tips. The white tipped scales are concentrated along the costa, and the black tipped scales are distributed evenly except towards the inner margin where they are more dense. The varying number of brown scales produces an effect ranging from a light shading to a predominantly brown color. The apical portion of the wing is clothed largely with white and light gray scales with white apices; specimens with extensive suffusing of brown in the basal area have some brown scales in the apical area as well.

A row of darker gray scales forms a conspicuous, straight, terminal line. Some individuals show three or four dark marks along the outer half of the costa, which appear to be areas accentuated by indistinct, diffuse strigulae. Wing length: males 9.2–11.5 mm ($n = 18$; mean = 10.2; s.d. = 0.47), females 8.3–9.7 mm ($n = 3$; mean = 9.2).

This species has a wide distribution, but its scarcity in collections suggests that it is either localized or overlooked because of its late flight period. We examined the following specimens: Canada. Manitoba: Aweme, 22 Sept 1921, N. Criddle (1♂, genitalia slide USNM 70001). Ontario: London, (4♂; genitalia slide USNM 70000). United States. Kentucky: Rowan Co., E side Rt. 1274, 2 mi W of Rt. 519, 8 Nov 1994, L.D. Gibson (1♂). Illinois: Putnam Co., 22 Oct 1946, M. O. Glenn (1♂), 25 Oct 1946 (1♂; genitalia slide MOG 219), 10 Oct 1949 (1♂), 16 Oct 1949 (2♂; genitalia slide DJW 103), 18 Oct 1949 (2♂), 29 Oct 1950 (2♂), 28 Oct 1964 (1♂), 24 Oct 1974 (1♂). Massachusetts: Hampshire Co., Amherst, Goodell, Fernald Coll. (2♂, 1♀; ♀ genitalia slide DJW 102). Ohio: Adams Co., 1 mi SE Lynx, 24 Oct 1991, L. D. Gibson (3♂; genitalia slide LDG 161), 25 Oct 1991, D. J. Wright (1♂; genitalia slide DJW 48), 4 Nov 1994 (20♂, 5♀), Athens Co., Ames Twn., 31 Oct 1990, H. T. Enterline (2♂; genitalia slides DJW 49, 50); Hamilton Co., Cincinnati, 3 Oct, A. Braun (♀, lectotype, genitalia slide C.H.), 7 Nov 1918, A. Braun (1♂, 1♀; ♂ genitalia slide USNM 69998, ♀ genitalia slide USNM 69999). Pennsylvania. Lackawanna Co., Scranton, 8 Nov 1905, A. E. Lister (1♂, paralectotype).

Phaneta ambodaidaleia Miller

(Fig. 6)

Phaneta ambodaidaleia, Miller 1983:101, figs. 12–14 (imago, female and male genitalia); Miller 1987:47 (figs. imago, male and female genitalia).

Miller (1983) described this species from Kentucky (Oldham Co.), Michigan (Ingham Co.), Missouri (Jasper Co.), North Carolina (Carteret Co.), and South Carolina (Charleston Co., type locality). The forewing ground color is creamy white, being most evident between the costa and radial vein. Between the radial and cubital veins, it has brownish ochreous longitudinal streaks extending from the base outward through the cell. From the distal edge of the cell to the termen the brownish ochreous streaks are between the veins, accentuating the creamy white on the veins. In most specimens the area between the cubitus and inner margin is suffused with brownish gray. The forewing is overlaid with a sprinkling of dark brown dots, accentuated on the apical half of costa and the outer margin. The dots on the outer margin occur between veins, creating the impression of an intermittent terminal line. Wing length: males 9–10.5 mm ($n = 24$; mean = 9.1; s.d. = 0.33); females 7.9–8.3 mm ($n = 4$; mean = 8.1).

We add the following records: Alabama: Baldwin Co., Bon Secour N.W. Ref., T9S, R2E, Sec 24, 18 Jan 1993 (1♂). Georgia: Clinch Co., DuPont, 19 Feb 1983 (1♀). Kentucky: Bullitt Co., N side Rt. 480, 6.9 mi E Rt. 61, 30 Mar 1993, L. D. Gibson (6♂; wing slide LDG 1), D. J. Wright (1♂). Mississippi: Hancock Co., Stennis Space Center, 27 Jan 1993, R. Kergosien (1♂); Harrison Co., Long Beach, 6 Feb 1994, R. Kergosien (3♂); Lee Co., Tombigbee State Park, 10–31 Mar 1993, R. Kergosien (1♂); Oktibbeha Co., 6 mi SW Starkville, 24 Feb 1985, R. L. Brown (1♂, genitalia slide RLB 1665), 2 Mar 1985 (4♂), 3 Mar 1985 (1♂), 9 Mar 1986 (1♂), T18N,R14E, Sec 33 SE, 2 Mar 1991 (3♂), 4 Mar 1991 (1♂), Mississippi State University North Farm, 6 Mar 1991 (1♀), T19N,R15E. Sec 16 [Black Belt Prairie], 5 Mar 1991, D. M. Pollock (1♂). Ohio: Adams Co., Lynx Preserve, 20 Mar 1991, D. J. Wright (4♂; genitalia slides DJW 47, 74), 1 mi SE Lynx, 20 Mar 1991, L. D. Gibson (4♂; genitalia slide LDG 162), 7 Apr 1992 (3♂), 26 Mar 1993, L. D. Gibson (1♂), D. J. Wright (4♂), 8 Apr 1993, D. J. Wright (4♂, 1♀). South Carolina, Charleston Co., McClellanville, 20 Mar 1968, R. W. Hodges (2♀; genitalia slides DJW 82, 102).

Phaneta canusana Wright, new species

(Figs. 7–9)

Description. *Head:* Scales on vertex, upper frons, and labial palpi brownish gray, shading toward white at their bases, with distinctly white tips. Antennae finely pubescent ven-



FIGS. 5–7. Males of *Phaneta* species from Adams County, Ohio. 5, *P. kokana*; 6, *P. ambodaidaleia*; 7, *P. canusana*, holotype.

trally, covered dorsolaterally with narrowly white-tipped, brownish gray scales. *Thorax*: Mesonotum and tegulae concolorous with head. *Forewing* (Fig. 7). Wing length: males 7.1–10 mm ($n = 39$; mean = 8.6; s.d. = 0.64), females 6.9–7.6 mm ($n = 4$; mean = 7.3). Dorsal vestiture a mixture of gray to brownish gray scales, mostly tipped with white, producing a unicolorous ashy gray appearance; some individuals with darker scales between veins and lighter scales on veins producing weakly highlighted veins and striate appearance; outer margin of wing with thin, distinct, dark gray terminal line at edge of wing membrane, accentuated by white bases of scales in basal row of fringe; fringe scales brownish gray with white apices. *Hindwing*: Upper side and fringe scales uniformly light brownish gray, with darker scales usually accenting the veins and wing margins. *Male genitalia* (Fig. 8): Tegumen widened dorsally; uncus reduced to rudimentary setose lobe; socii short, slightly flattened, with lateral margin convex, median margin concave; aedeagus short, with more than 20 cornuti; juxta with short caulis, anellus not closely surrounding aedeagus ventrally; valva with base of sacculus sparsely setose, with large group of dense setae on basal medial area, neck sparsely setose on ventral margin, cucullus sub-triangular with median surface angled from dorsal edge of valva and overlapping neck ventrally (13n). *Female genitalia* (Fig. 9): Sternum VII densely scaled on anterolateral and posterolateral corners and medial area anterior to ostium, sparsely scaled elsewhere, anteriorly rugose; tergum VIII sparsely setose on lateral extensions and posterior half of dorsum, scales absent; papillae anales facing laterally, setae sparse on medial and dorsal areas of pads, more dense on ventral margins; lamella postvaginalis with lateral margins slightly concave, with shallow longitudinal groove medially, with four or five setae in irregular pattern, microtrichiate throughout; ductus bursae with moderately sclerotized colliculum posterior to inception of ductus seminalis; width of smaller signum less than one half greatest width of larger signum (2n).

Types. *Holotype* ♂, "OH: Adams Co., Lynx Prairie Preserve, Station 6, March 17, 1989, leg. D. J. Wright." Type locality at 38°45'40"N 83°24'46"W. The holotype is deposited in USNM. *Paratypes*. Kentucky: Bullitt Co., Co. Rd. 480, 7 mi E of Shepherdsville, 30 Mar 1993, D. J. Wright (1♂, 1♀; ♀ genitalia slide DJW 104), N side Rt. 480, 6.9 mi E Rt. 61, 30 Mar 1993, L. D. Gibson (1♂); Rowan Co., E side Rt. 1274, 2 mi W Rt. 519, 13 Mar 1995, L. D. Gibson (9♂, 2♀). Mississippi: Oktibbeha Co., T19N, R15E, Sec. 16 [also known as "Osborn Prairie"; 33°30'41"N 88°44'08"W], 10 Feb 1991, Black Belt Prairie, D. M. Pollock (5♂), 13 Feb 1992, R. L. Brown (5♂), 2 Feb 1995, R. L. Brown (1♂). Missouri: Benton Co., 3 miles NW of Warsaw on State Hwy UU [data are inaccurate as Hwy UU intercepts State Highway 7 at 5 miles NW of Warsaw], 28 Feb 1976, J. R. Heitzman (1♂; genitalia slide D. Hagler 924803), 2 Mar 1976, J. R. Heitzman (2♂; genitalia slides D. Hagler 610801, 729802). Ohio: Adams Co., Lynx Prairie Preserve, 17 Mar 1989, D. J. Wright (1♂, 1♀, ♂ genitalia slide LDG 78, ♀ genitalia slide W. E. Miller 1112921), 1 mi. S. E. of Lynx, 20 Mar 1991, L. D. Gibson (4♂, genitalia slide LDG 160), D. J. Wright (1♂, genitalia slide DJW 76), 2 Mar 1992, D. J. Wright (7♂; genitalia slides DJW 51, 52, 75, W. E. Miller

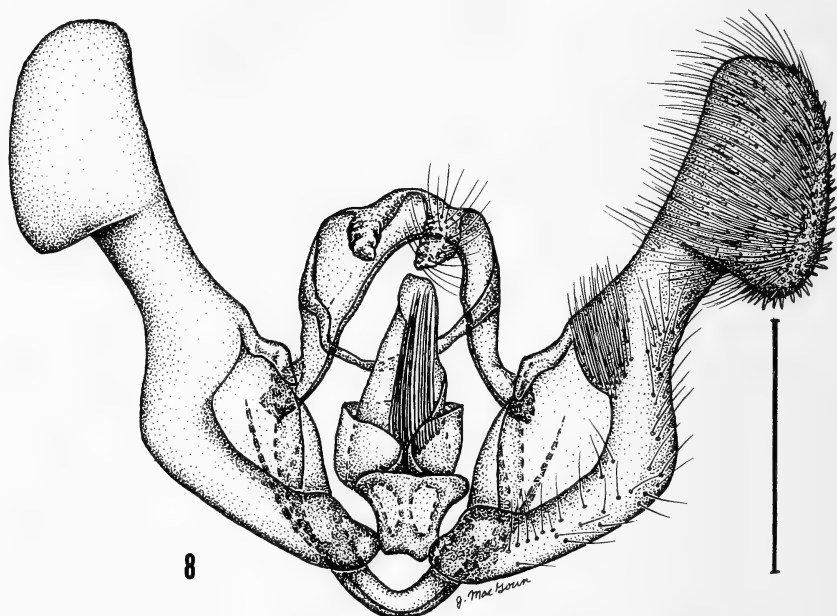


FIG. 8. *Phaneta canusana*, male genitalia. Adams County, Ohio, slide W. E. Miller 1112922. Scale line 0.5 mm.

812922, 1112922), 4 Mar 1992, L. D. Gibson (3♂; wing slide LDG 2), 26 Mar 1993, L. D. Gibson (1♂), D. J. Wright (5♂), 8 Apr 1993, D. J. Wright (3♂). South Carolina: Greenville, 23 Feb 1982, Richard S. Peigler (1♂; genitalia slide R. L. Brown 1565). Paratypes are deposited in collections of DJW, Cincinnati, OH, LDG, Florence, KY, JRH, Independence, MO, AMNH, CNC, MEM, USNM, ZM, Copenhagen [R. Peigler donation].

Diagnosis. *Phaneta sublapidana* and *P. lapidana* are western species with fall flight periods. Heinrich (1923) considered them to be closely related, apparently based on Walsingham's descriptions and an examination of a cotype of *Semasia sublapidana*. He separated them in his key by Walsingham's description of the setation of the male antennae, stating that it is "strongly pubescent" in *sublapidana* and "nearly smooth" in *lapidana*. He later obtained specimens of *P. lapidana* from British Columbia and commented (1929) "*lepidana* [sic] resembles *kokana* Kearfott, which may be nothing but an eastern variety." The male specimen of *P. sublapidana* that we examined has dense setae covering about two-thirds the circumference of each flagellomere, the setae being subequal in length with the width of the flagellomere. The female of *P. sublapidana* has sparse setae restricted to less than a third of the flagellomere circumference, and the setae are much shorter than the flagellomere's width. The male specimen of *P. lapidana* that we examined has a narrow strip on the ventral surface of each flagellomere covered with setae that are subequal in length with the width of the flagellomere. The remainder of the circumference of the flagellomere is covered with white scales. Although the forewing ground color is similar in both species, *P. sublapidana* differs from *P. lapidana* and *P. canusana* in having a contrasting light apical area beyond the discal cell in which light gray scales are intermixed with grayish orange and light brown scales. *Phaneta sublapidana* differs from the other species treated here in having male genitalia with a deep and wide ventral emargination of the valval neck (Fig. 2). *Phaneta lapidana* is similar to *P. canusana* in both forewing color and male genitalia.

Phaneta kokana, *P. canusana* and *P. ambodaidea* are eastern species that are sym-

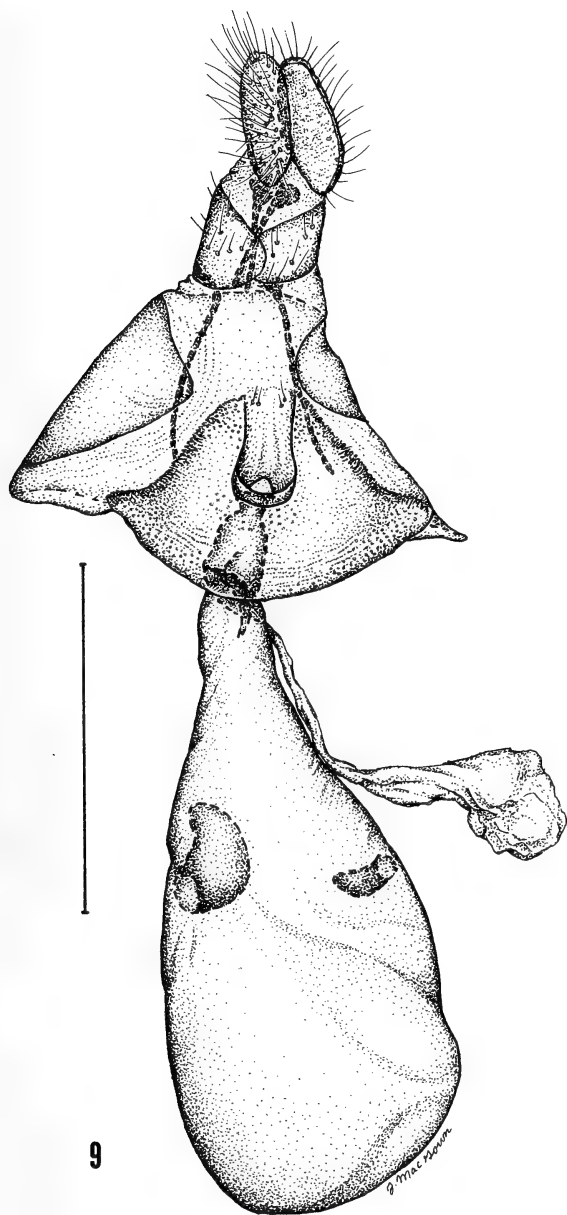


FIG. 9. *Phaneta canusana*, female genitalia. Bullitt County, Kentucky, slide D. J. Wright 104. Scale line 1.0 mm.

patric in at least part of their ranges. They have been collected at a single site in Adams Co., Ohio. Their genitalia are similar. In males of *P. ambodaidaleia*, the basal portion of the cucullus that overlaps the valval neck has a convex margin. This margin is straight from the ventral corner of the cucullus to the neck in the other two species. Wing color and flight period provide reliable means of differentiating the three species. The ground color of the forewing in *P. ambodaidaleia* is creamy white, and that of *P. kokana* and *P. canusana* is gray. In *P. kokana* the ground color is suffused with light brown scales in the basal area and white or white tipped scales in the apical third of the wing, thereby distinguishing its appearance from that of *P. canusana*, which is unicolorous gray. Mean forewing lengths of males of the three species differ significantly, with *P. canusana* being the smallest and *P. kokana* the largest. The flight period of *P. kokana* varies from late September to early November, depending on latitude, whereas *P. ambodaidaleia* and *P. canusana* fly in the spring. Earliest capture dates for *P. ambodaidaleia* range from January on the Gulf Coast in Alabama and Mississippi to February 24 in Oktibbeha County, Mississippi and March 20 in Adams County, Ohio. In Ohio the flight period of *P. canusana* begins one to two weeks earlier than that of *P. ambodaidaleia* and partially overlaps the latter in late March and early April. A similar staggering of flight periods occurs in Mississippi, although no overlap has yet been recorded.

Habitat. *Phaneta canusana* appears to be associated with a habitat supporting prairie vegetation, based on extensive collecting in various physiographic regions in Ohio, Kentucky, Missouri, and Mississippi. The Lynx Prairie Preserve and adjacent collection site one mile SE of Lynx are among an extensive group of small openings in the otherwise forested ridge tops and valleys of the unglaciated portion of southern Ohio. The Kentucky sites in Rowan and Bullitt Counties are similar, but do not possess the plant diversity of the Ohio localities. The Missouri specimens come from the vicinity of the Osage Plains, which contains many of the state's native prairies, and the single South Carolina specimen was collected at a porch light in a developed suburb of Greenville. The latter locality was originally wooded, and in 1982 the nearest open habitat supporting prairie plants was about three miles distant from the collection site.

The preference for a prairie habitat is supported by collections in the Black Belt physiographic region of Mississippi, an area discretely defined by an underlying layer of Selma Chalk that extends in a crescent shape from northern Mississippi to southeastern Alabama. Nine prairie remnants in the Black Belt of Mississippi have been sampled with blacklights on 93 nights since 1990; of these, three remnants were sampled on 16 nights in January, February, and March. *Phaneta canusana* was collected at the Osborn prairie remnant on three of the four nights during February but not in January or March. Neither *P. canusana* nor *P. kokana* was collected at this site during eight nights in September, eight nights in October, and four nights in November. Other types of habitats in the Lower Coastal Plains, Jackson Prairie, Alluvial Plain, Loess Hills, and Flatwoods physiographic regions (as mapped in Testa and Lago, 1994) have been extensively sampled over many years during January–March without producing records of the new species. Larval hosts have not been recorded for any of the five species discussed in this paper, but they probably are Asteraceae, as is the case with other species in the genus.

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THREE ADDITIONAL *BACTRA* IN CALIFORNIA, ONE NATIVE BUT OVERLOOKED, ONE PROBABLY INTRODUCED, ONE NEW SPECIES (TORTRICIDAE)

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ABSTRACT. *Bactra maioriana* Heinrich, which was not recorded west of Utah previously, *B. priapeia* Heinrich, a Gulf Coast species believed to have been introduced into coastal southern California, and *B. miwok*, new species (TL: China Camp, Marin Co.) are recorded. Diagnostic features for these and the two previously recorded species, *B. verutana* Zeller and *B. furfurana* (Haworth) are illustrated. Adults of *B. miwok* appear to be diurnal; early instar larvae mine leaves of *Cyperus* and presumably *Carex*.

Additional key words: Olethreutinae, range expansion.

Members of the genus *Bactra* Stephens (Tortricidae: Olethreutinae, Bactrini) are relatively narrow winged, mainly tan tortricids that resemble crambids when at rest. Larvae of several species in the Palaearctic, Nearctic, Hawaii, and India, feed in stems of *Carex*, *Cyperus*, *Scirpus* and other sedges (Cyperaceae), *Juncus* (rushes, Juncaceae), and *Typha* (cat-tails, Typhaceae) (Emmet 1979, Frick & Garcia 1975, Heinrich 1926, Fletcher 1932, Zimmerman 1978). There are more than 50 described species of *Bactra*, distributed primarily in pantropical and subtropical regions. Most of the species are both variable in forewing pattern and similar to one another, so that study of the genital structures is necessary to differentiate them. Diakonoff (1956, 1962, 1963, 1964, 1973) has illustrated most of the species with excellent, detailed drawings.

Parallel variation in forewing pattern was categorized and illustrated with photographs by Diakonoff (1962). The forewings show a complex pattern of pale and dark transverse markings ('fasciate type', considered by Diakonoff to be primitive and retained only in *B. furfurana*) or within a species often they are unicolorous tan or brown or may feature variable maculation ('maculate type') and/or a broad, dark dorsal half or median band from base to apex ('vittate type'). Most species display at least the unicolorous and vittate types.

Six species of *Bactra* occur in America north of Mexico, of which two have been recorded in California (Heinrich 1926, Diakonoff 1964):

Bactra verutana Zeller (TL: Dallas, TX) occurs throughout much of North America and is recorded in Puerto Rico, Paraguay, and South Africa (Diakonoff 1964). In California it is widespread at lower elevations, including coastal areas, Central Valley, and deserts (CAS, CDEA, LACM, UCB, UCD; see acknowledgements). The California race was designated as *chrysea* Heinrich (1926), but as pointed out by Diakonoff (1964), there is no justification in applying a subspecies name to any

subset of these variable populations. *B. verutana* often is numerous at lights and presumably is multivoltine (e.g., there are records for every month from April to December in the San Francisco East Bay area). Most collections have been made in July, August and September. The adults are small (male forewing length 5.6–8.4 mm, female 6.8–9.5 mm) and usually have a more or less unicolorous tan forewing or with reduced blackish maculation; a few exhibit the 'vittate type' pattern with a longitudinal dark streak. The genitalia of both sexes are diagnostic (Figs. 1, 6). The larvae feed in sedges, especially *Cyperus*, including weedy species, and the biology has been extensively studied in relation to possible biological control of nutsedges (Poinar 1964, Frick & Garcia 1975).

Bactra furfurana (Haworth) (TL: England) is a Holarctic species that also occurs widely in California but is more localized and less often encountered. Most of the records are more northern (North Coast, inland Mendocino Co., Sacramento Valley), although *B. furfurana* has been taken at La Jolla, San Diego Co. and Bishop, Inyo Co. (UCB). It appears to be absent from Lower Sonoran zones in the San Joaquin Valley and desert areas. The voltinism is not documented in California; collection records range from late April (Hopland Field Sta., Mendocino Co.) to mid July (Bishop), but there has not been seasonal monitoring at one locality. I have not seen *B. verutana* and *B. furfurana* occurring in close sympatry. The forewing, which is dark with variable pale markings ('fasciate type') and has a more acute apex, distinguishes *B. furfurana* from the other California species, as do the genitalia (Figs. 2, 7).

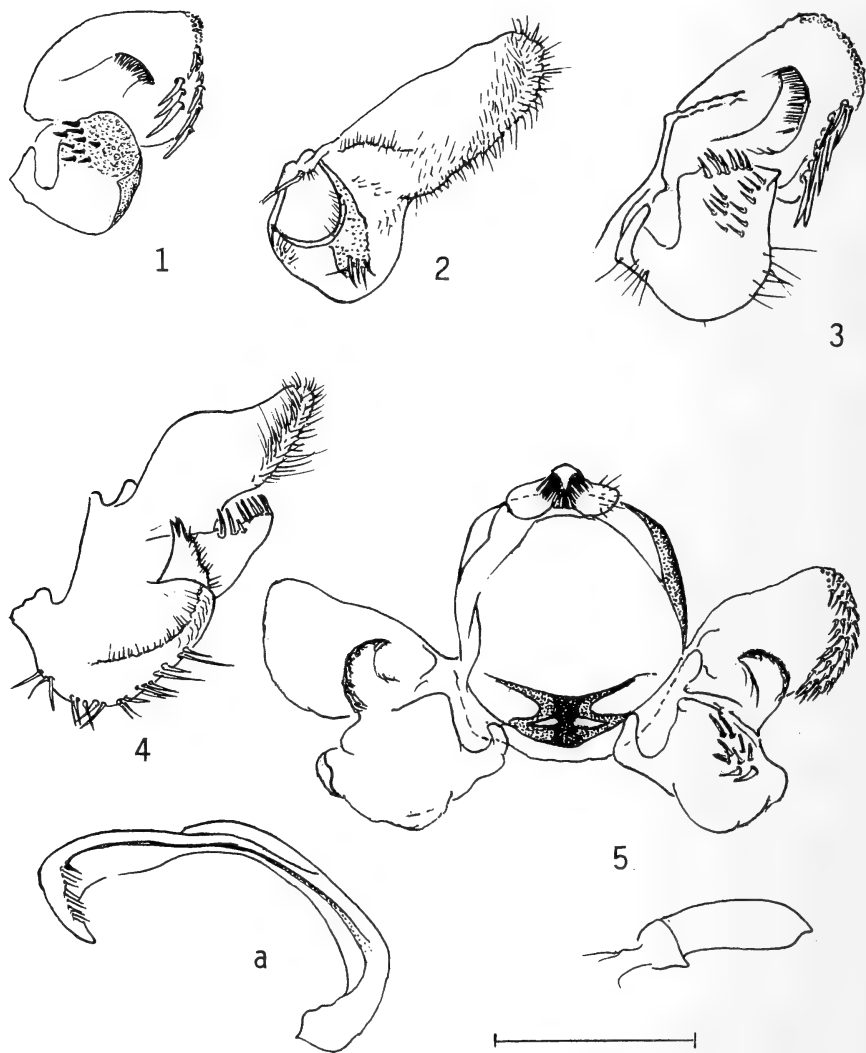
Three additional species have been confirmed as resident in California: *Bactra maioriana* Heinrich, which is a widespread but rarely collected, presumably native species; *B. priapeia* Heinrich, likely an introduced species in coastal southern California; and *B. miwok*, new species, the male of which has been known for 35 years, the female only recently.

Bactra maioriana Heinrich

Bactra maioriana, Heinrich 1923, Proc. Entomol. Soc. Washington, 25:105 (TL: VA).

This species is a widespread, apparently native, Nearctic insect. Diakonoff (1964) presented illustrations of the diagnostic genitalia and regarded *B. maioriana* to be distinct from any Old World species. The species is recorded in the Great Lakes region (Miller 1987) and westward to North Dakota (UCB) and Utah (Heinrich 1926). The larvae are reported to feed in stems of *Scirpus* and *Typha* (Heinrich 1926, Diakonoff 1964).

The Utah records, paratypes collected at Vineyard in 1914 and 1922, and Bear River Bay, Great Salt Lake (Braun 1925), are considered to represent native populations. No other western representatives were recognized until we took specimens at the Antioch National Wildlife Refuge, Contra Costa Co., Calif., in July 1990. At this site, both *Scirpus californicus* (C. Meyer) and *Typha latifolia* L. grow along the San Joaquin River. Because this is a shipping route, an introduction via cargo ships in recent times seemed to be a plausible explanation for the discovery of this disjunct population. During search of collections, however, I recovered additional records of *B. maioriana* from disparate parts of California. The widespread occurrence suggests that this species is native in the Pacific States but



FIGS. 1-5. Male genitalia of *Bactra* species. 1, *B. vertutana* Z., valva, inner aspect (JAP prep. 6413, Bowman, Placer Co., Calif.); 2, *B. furfurana* (Haw.), valva (redrawn from Diakonoff 1956, Europe); 3, *B. maioriana* Heinr., valva (redrawn from Diakonoff 1964, paratype); 4, *B. priapeia* Heinr., valva and **a**, aedeagus drawn to same scale (redrawn from Diakonoff 1964, holotype); 5, *B. miwok* Powell, ventral aspect, aedeagus removed and shown dorsolateral aspect (holotype). [scale = 0.5 mm for Fig. 5].

has been overlooked, perhaps in part owing to its superficial similarity to the more abundant *B. vertutana*. Individuals of *maioriana* tend to be larger (male 8.2 mm forewing length, female 8.5–10.5 mm in California examples) and darker colored, with a greater frequency of vittate type, but there is overlap in forewing phenotype. The two are sympatric at Antioch and Bundy Canyon, Riverside Co. Available records (Diakonoff 1964,

Miller 1987, present data) suggest a univoltine cycle, adults flying in late spring to early summer.

The male genitalia are similar to those of *B. verutana* and *B. miwok* (see diagnosis of latter, Figs. 1,3,5), while the female has distinctive, heavily sclerotized, rugose patches laterally in the VIII–IX intersegmental membrane (Fig. 8).

California data: Contra Costa Co.: Antioch National Wildlife Refuge, 1♂, 1♀ VII-10-90, at blacklight (Y.-F. Hsu & J. Powell, UCB) [JAP genit. preps. 6371, 6372]. Monterey Co.: Castroville, 1♀ VI-2-61 (W. H. Lange, UCD) [JAP prep. 6420]. Riverside Co.: Bundy Cyn. 1660', 9 mi. S Perris, 1♀ VII-20-76 (R. J. Ford, LACM) [JAP prep. 6405]. San Luis Obispo Co.: La Panza Campground, 12 mi. NE Pozo, 1♀ V-2-62 [at lights] (J. Powell, UCB) [JAP prep. 6449].

Bactra priapeia Heinrich

Bactra priapeia, Heinrich 1923, Proc. Entomol. Soc. Washington 25:105 (TL: LA).

This species has been recorded from Florida, Louisiana, the Gulf Coast of Texas, British Honduras, and Panama (Heinrich 1926, Diakonoff 1964). The adults are larger than any other North American *Bactra* (male 9.3 mm forewing length, female 10.1–10.9 in California examples), and the genitalia are markedly distinct in both sexes (Figs. 4, 9). Forewings of California specimens are pale, rusty, or dark tan without distinct markings, but maculate and vittate examples are reported by Diakonoff. The larval hostplant has not been recorded.

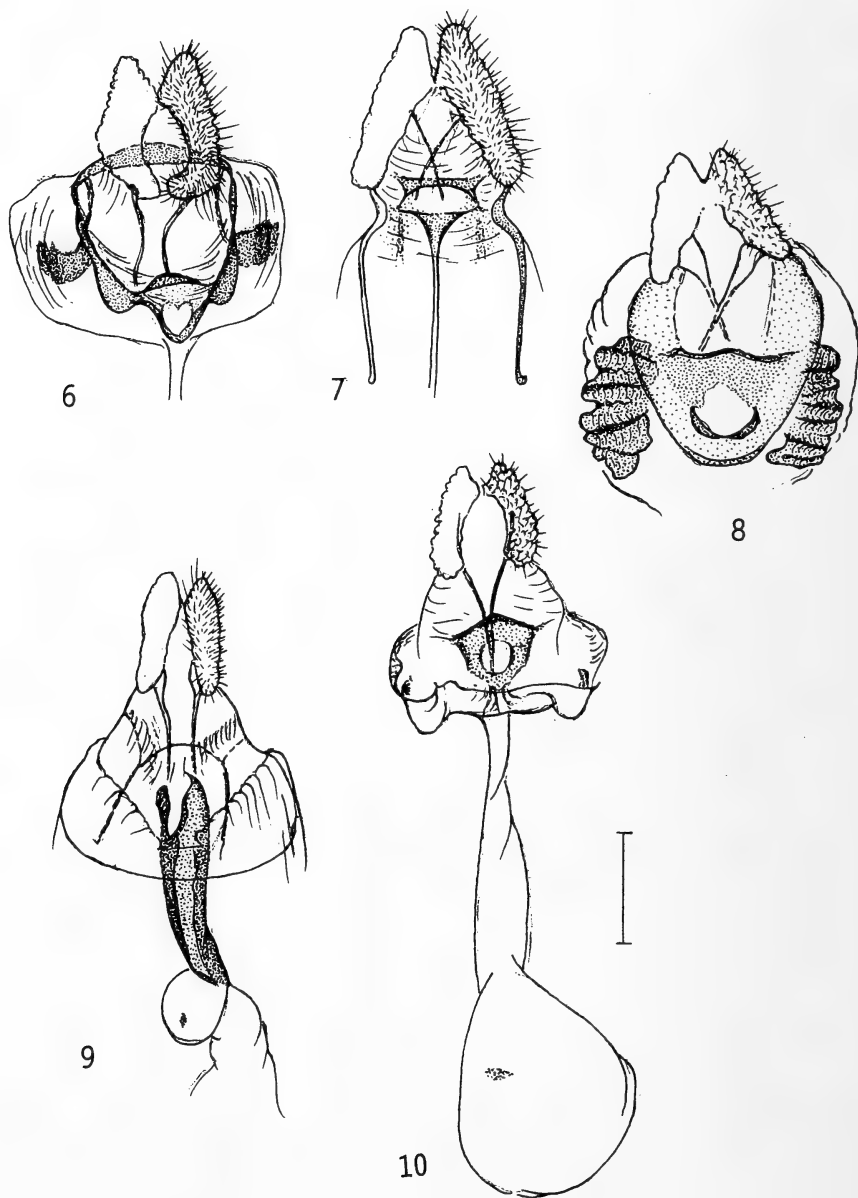
During a light trapping survey by the San Diego County Department of Public Health in 1959, R. A. Mackie recovered one female of *B. priapeia* at Mission Bay, an area subsequently converted from marshland to parks. Although I identified the species in 1960, it was not until 1987 that another record was obtained to confirm the residency of this species in California. Because the previous collection records are from areas adjacent to the Gulf of Mexico, it seems likely that *B. priapeia* is introduced in coastal southern California.

California data: Orange Co.: Aliso Cr., 0.5 km E Highway 1, nr. South Laguna, 1♂, 2♀ X-7/8-87, at lights (J. Powell, UCB) [JAP genit. preps. 6445, 6446]. San Diego Co.: Mission Bay, 1♀ IX-30-59, light trap (R. A. Mackie, UCB) [JAP prep. 501].

Bactra miwok Powell, new species

Description. A small, almost uniformly dark brown species with only indistinct ochreous mottling on the forewings of some individuals. *Male*: forewing (FW) length 5.9–7.9 mm (30n); length 3.2–3.4 × width; termen strongly angled, nearly straight, very slightly convex, apex produced. Color of head and palpi concolorous with FW, in fresh specimens variable, dark brown tinged with dark ochreous-tan to dark rust-brown; pale examples faintly irrorate with pale ochreous, not defining a visible FW pattern. No 'maculate' or 'vittate' polymorphism known. FW underside gray, fringe pale rust-ochreous. Hindwing entirely dark gray, fringe pale gray, underside the same. Abdomen scaling dark shining gray, venter slightly paler gray. Genitalia (Fig. 5, drawn from holotype, JAP prep. no. 6390; 5n), similar to *B. maioriana* and *verutana*, with the major spurs of the cucullus slender, numerous (ca. 30), and broadly distributed along distal margin and posteriorly; major spurs of the valva basally fewer (10–12), also slender; saccular margin broadly expanded laterally. *Female*: FW length 6.3–7.0 mm (2n), length to width ratio within range of male. Phenotype similar to male, color probably comparably variable. Genitalia (Fig. 10, drawn from JAP prep. 7157; 2n), similar to *B. verutana*, but the ring around IX and lateral patches on the intersegmental membrane of that species only weakly sclerotized, lateral lobes more widely separated and displaced anteriorly from sterigma.

Types. *Holotype* ♂: CALIF: China Camp, Marin Co., April 18, 1959 (J. Powell) [JAP genit. prep. 6390]. *Allotype* ♀: CALIF: Miwok Meadow, China Camp St. Park, Marin Co., March 30, 1995 (J. Powell) [JAP prep. 7089]; both in UCB. *Paratypes* (30): CALIF: Marin Co.: same data as holotype, 1♂ [JAP prep. 555]; Miwok Mdw., China Camp St. Park, 2♂ III-30-94, 12♂ V-2-94, 9♂, 1♀ III-30-95 (J. Powell) [JAP preps. 7088 ♂, 7157 ♀]; Ring Mt., 1♂ III-30-85, 1♂ IV-11-94 (J. Powell). Monterey Co.: Asilomar, 1♂ V-17-59 (G. I. Stage)



FIGS. 6-10. Female genitalia of *Bactra* species: VIII-IX segments, sterigma, sclerotization of intersegmental membrane, and basal portion of ductus bursae, ventral aspect. **6**, *B. verutana* (JAP prep. 6950, Coachella Vy., Calif.); **7**, *B. furfurana* (Haw.) (JAP prep. 7194, Smartville, Calif.); **8**, *B. maioriana* Heinr. (redrawn from Diakonoff 1964, paratype); **9**, *B. priapeia* Heinr. (redrawn from Diakonoff 1964, Texas); **10**, *B. miwok* Powell (JAP prep. 7157, China Camp). [scale = 0.5 mm for Fig. 10].

[JAP prep. 7158]. Santa Clara Co.: 3 mi W New Almaden, 1♂ IV-18-69 (P. A. Opler) [JAP prep. 7162]. Sonoma Co.: Bodega, 1♂ V-3-36 (E. C. Johnston, USNM). Paratypes will be deposited in CDFA, CNC, LACM, Mississippi State U., U. Minnesota, USNM.

Diagnosis. The male genitalia of *B. miwok* are similar to *B. verutana* and *B. maioriana*, but the new species has more major spines of the cucullus (ca. 30), which are more broadly distributed distally and extended to the anterior margin; in *verutana* and *maioriana* these spines are less numerous (10–12), much stouter and arranged in two separated lines in *verutana* (Fig. 1), restricted narrowly to the distal margin and not reaching the posterior margin in *maioriana* (Fig. 3). The major spines of the basal part of the valva are quite short in *verutana*, varying from 6–8 to 15–20 among individuals, while they are longer and slender in *maioriana* and *miwok*, fewer in the latter (12–14) than in *maioriana* (22–24). The distal margin of the sacculus is more broadly expanded laterally in *miwok* than in the other two species, which have attenuated marginal extensions. In female genitalia and associated structures, the new species most closely resembles *B. verutana* (Fig. 6), with the sclerotized areas lateral to the sterigma reduced compared to that species, the lateral cup-like structures more widely separated and displaced anteriorly to the sterigma (Fig. 10). The other three species discussed differ greatly in these structures (Figs. 7–9).

Biological Notes. The new species apparently is univoltine, available records of adults spanning late March to mid May. There has not been thorough survey to preclude a summer generation, but I made visits to Ring Mountain in late May, July, and September, and Miwok Meadow in late August. The vegetation was very dry and no *Bactra* were recovered from either site.

Lack of light attraction records suggests that this species is diurnal. The moths were netted during midday and early afternoon, and a few were observed to fly in direct sunshine without observer disturbance. Efforts to observe adults during crepuscular and matinal hours produced negative results. I visited the Miwok Meadow colony site on 10 April 1994 between 1810–1910 hr PST, just before and after sundown, and on 24 May 1994 at 0530–0615 hr PST. Observations of caged adults (5♂, 1♀) were inconclusive as to the normal diel periodicity. Adults remained 'alert' with the antennae erect during daylight hours and occasionally actively ran towards the light. It appeared they became more active in late afternoon sunshine and at dusk, but several moved after dark. Neither mating nor oviposition was observed, but the female deposited about 100 eggs during a 5-day period.

At Miwok Meadow adults occurred in a wet seepage meadow above tidal marshes along San Francisco Bay, in association with three species of *Carex* (*C. multcostata* Mackenzie, *C. praegracilis* Boott, and *C. tumulicola* Mackenzie) and *Juncus* ?*patens* E. Meyer, while at Ring Mountain they were taken in a narrow seepage gully on a steep slope in serpentine grassland, with what appeared to be one of the same and a fourth species of *Carex*, and both *Cyperus* and *Juncus*. However, no definite association with any one of the plants was observed, and pupal shells were not found. None of these plants has a sufficiently robust stem to support later instar larvae, particularly through winter, and I assume that late instar larvae feed at the base of the plant.

Early instar larval activity of *Bactra miwok* in the laboratory suggests that the larval biology is similar to that described for *B. verutana* by Poinar (1964). Eggs of *B. miwok* were deposited in variable clumps of usually 4 to 8 eggs (sometimes singly), usually regularly overlapped in pairs so that groups of 4, 6, or 8 were formed. The female, caged with a bouquet of two species of *Carex* from the field site, selected the semitranslucent, bract-like blades that subtend the green foliage as oviposition sites. No eggs were laid on inflorescences nor on the glass sides of the container. Incubation was rapid, requiring 6–7 days until hatching at 17–21° C. Poinar reported 3–4 days in *B. verutana* at 22° C. Provided with foliage of *Cyperus eragrostis* Lam., a native plant that behaves like a weed and has much larger leaves than the China Camp *Carex* species, the first instar larvae tunneled downward from cut leaf ends, in straight mines between the leaf veins. The frass-packed mines were visible within 2 days of hatching and reached 4–6 cm in length by day 4; by day 7 the leaves were drying and had folded along the midrib, and 2nd instar larvae made holes to the surface and fed between the folded leaf blade or entered new mines. According to Poinar (1964), mining in *B. verutana* extends down to the basal meristematic portion of the stem, where larvae complete development in 8–11 days in the lab at 24° C.

Larvae of *B. miwok* were not maintained on entire plants that would have enabled completion of feeding.

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Cooperation by Richard A. Coleman, San Francisco Bay Refuge Complex, U. S. Fish and Wildlife Services, Newark; Kenneth Leigh, California Department of Parks and Recreation, San Rafael; and Larry Serpa, The Nature Conservancy, Tiburon, permitted survey at the Antioch National Wildlife Refuge, China Camp State Park, and Ring Mountain Reserve, respectively. I thank the curators of the following collections, whose cooperation facilitated my search of unidentified accessions and curated material for *Bactra*: California Academy of Sciences, San Francisco (CAS); California State Department of Food & Agriculture, Sacramento (CDFA); Los Angeles County Museum of Natural History, Los Angeles (LACM); San Diego Museum of Natural History, San Diego (SDNH); University of California, Davis (UCD); Essig Museum, University of California, Berkeley (UCB). R. A. Mackie, now of Concord, CA, provided specimens from an extensive light trapping program with the San Diego County Department of Public Health in 1959, which are deposited in UCB. Barbara Ertter and Dan Norris, University Herbarium, UC Berkeley, provided plant identifications.

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A NEW *CHAETAGLAEA* FROM THE SOUTHEASTERN UNITED STATES (NOCTUIDAE: CUCULLIINAE)

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ABSTRACT. *Chaetaglaea fergusoni*, new species, is described and illustrated, and compared to other members of the genus. *Chaetaglaea tremula* and *Chaetaglaea sericea* are reported as new from Louisiana.

Additional key words: Mississippi, South Carolina, voltinism, winter moths.

In 1943, Franclemont described the genus *Chaetaglaea*, listing three species: *C. cerata* Franclemont, *C. tremula* (Harvey), and *C. sericea* (Morrison). Hodges (1983) retained the same treatment for the genus. Both Franclemont (1943) and Forbes (1954) stated that only *C. tremula* ranged south to the Gulf coastal states, and Covell (1984) indicated that both *C. tremula* and *C. sericea* occurred in the Gulf coastal states from Florida to Mississippi. The genus *Chaetaglaea* has not been reported previously from Louisiana by noctuid workers (see von Reizenstein 1863, Jones 1918, Folsom 1936, Glick 1939, Harrison 1946, Merkl and Pfrimmer 1955, Pfrimmer 1957, Chapin & Callahan 1965). The purpose of this paper is to describe a new *Chaetaglaea* from Louisiana, and to provide new distributional and phenological data for the genus from the southern United States.

Chaetaglaea fergusoni Brou, new species (Figs. 1, 2)

Description. *Male* (Fig. 1A): Mean forewing length 19.6 mm (range 18.9–20.4 mm, $n=13$). *Head*: color medium or reddish brown, with orange hue, frontal tuft rounded; palpi color contrasting reddish brown or orange brown; antennae similar matching color, simple, slender, acuminate. *Thorax*: frontal area dorsal color similar to head, orange brown scales less numerous caudally, color becoming reddish brown; scales form longitudinal central ridge; ventral color reddish brown; legs reddish brown to orange brown, usually similar to color of palpi. *Abdomen*: dorsal color rich reddish brown, on aged specimens brown to tan, generously peppered with black scales which substantially increases caudally; ventral color same as dorsal; anal tuft orange brown. *Forewing*: dorsal ground color rich monochrome reddish brown, light dusting of pale whitish scales basad of postmedial line, especially concentrated along costal margin near base; same area peppered with numerous, well dispersed, inconspicuous, black scales; whitish scales form a barely noticeable, thin line distally hugging postmedial line; single reniform spot, dark and small, sometimes nearly distinguishable or nonexistent; basal line usually limited to dark dash or spot on costal margin, occasionally extending onto basal area of discal cell; dark antemedial line extending from costal edge to a point about one-third width of wing, directed toward anal angle, abruptly changing direction perpendicular to inner margin, increasingly obscure, often vanishing; similar medial line roughly parallel to antemedial line, curving basally approaching inner margin; similar postmedial line beginning at costal edge, roughly parallel to medial line, usually vanishing two-thirds distance to inner margin, but occasionally represented by short dash near costal margin or distinct dark line intersecting inner margin; subterminal line changes from rich reddish brown ground color to area completely and



FIG. 1. *Chaetagnalea fergusoni*, new species. A, male holotype; B, female allotype.

delicately burnished with lighter shiny brown scales, creating whitish suffusion to outer margin, distinct to nearly indistinguishable; dark zigzag terminal line inwardly accented by tiny black dots between each vein, representing adterminal line, sometimes only adterminal dots evident; fringe uncontrasting reddish brown; ventral color fuscous, center bordered by shiny reddish brown along costal margin and broader area along outer margin; maculation limited to postmedial line, prominence variable. *Hindwing*: dorsal color fus-

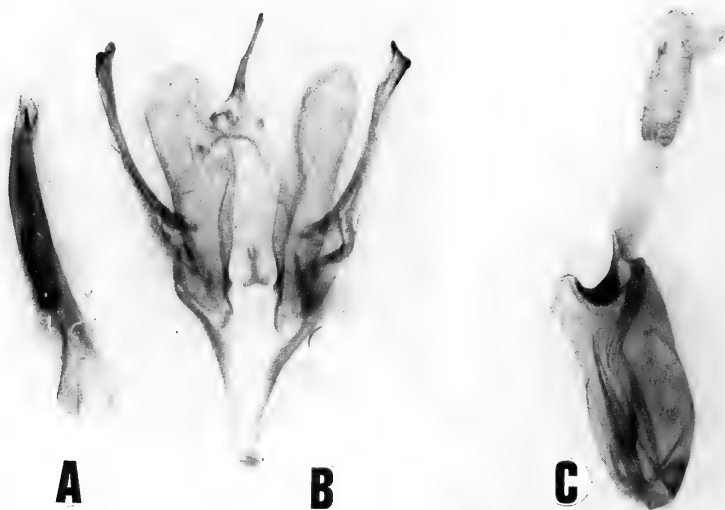


FIG. 2. Genitalia of *C. fergusoni*, Mississippi, Harrison County. A, B, male (aeodeagus at left); C, female.

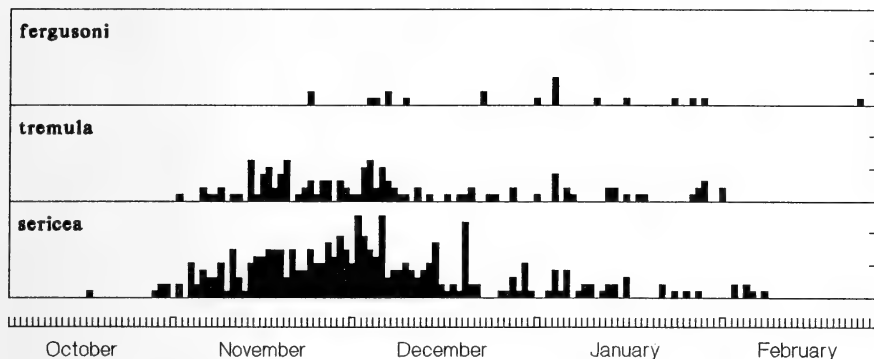


FIG. 3. Dates of capture for *Chaetaglaea* taken at Section 24, Township 6, South Range 12 East, 6.8 km NE Abita Springs, Louisiana. Vertical tick marks represent five captures: for *C. fergusonii*, $n = 20$, 1984–1996; for *C. tremula*, $n = 118$, 1990–1995; for *C. sericea*, $n = 303$, 1990–1995.

cous postmedially, increasingly lighter tan antemedially approaching base and anal area; fringe contrasting light brown, bordered inwardly by fine, inconspicuous, sinuous, reddish brown line, itself bordered basally by similar lighter contrasting, fine, tan line; still further bordered basally by edge of fuscous wing area, sometimes appearing as distinct adterminal line, often accented between some veins as tiny black dots; ventral color shiny reddish brown, peppered with well dispersed individual black scales; area near inner margin more fuscous; continuation of forewing postmedial line is only maculation. *Genitalia* (Fig. 2A–B, $n=3$): valves bilaterally asymmetrical; right valve simple, elongate, narrow, cuneate, cucullus truncate; left valve simple, elongate, narrow, cucullus obtuse; aedoeagus lanceolate, curving near obtuse apex, single tiny cornutus; large, elongate, spatulate, free lobes of sacculus extending almost to valve ends; uncus slender, acuminate; saccus greatly elongate, tapering to truncate end. *Female* (Fig. 1B): Mean forewing length 19.4 mm (range 19.0–19.9 mm, $n=5$). External morphology as described for male. *Genitalia* (Fig. 2C, $n=2$): oval unisaccate corpus bursae, small appendix bursae, separated distally by heavily sclerotized crescent patch. Sclerotized distal half of ductus bursae.

Types. *Holotype* ♂ (Fig. 1A): USA, Louisiana, St. Tammany Parish, 4.2 miles (6.8 km) NE Abita Springs, Section 24 of Township 6, South Range 12 East, 7 December 1988. *Allotype* ♀ (Fig. 1B): same locality as holotype, 1 January 1992. *Paratypes*: 13 ♂ 3 ♀, same locality as holotype, 24 November to 24 February 1984–1996; 5 ♂ 7 ♀, Mississippi, Harrison County, 20 December to 10 January 1992–1993; 1 ♂, Mississippi, Hancock County, 16 February 1992; 1 ♀, South Carolina, Charleston County, Wedge Plantation, South Santee River, 22 November 1967. Holotype and allotype deposited at the U.S. National Museum of Natural History, Washington, D.C. Paratypes deposited at Louisiana State University, Baton Rouge, and in the private collections of Rick Kergosien and the author.

Etymology. I take pleasure in naming this species in honor of Douglas C. Ferguson, who appears to have first discovered it 30 years ago.

Diagnosis and Discussion. *Chaetaglaea fergusonii* looks most similar to *C. tremula*. The maculation of both species can be nearly identical, although some specimens of *C. fergusonii* tend to have less accentuated markings. *C. tremula* is highly variable in both color and maculation, but despite this, *C. fergusonii* can always be separated by its less variable, rich reddish brown coloration. The male genitalia of *C. fergusonii* also differ from the three other species in the genus. Franclemont (1943) and Forbes (1954) illustrated and discussed the male genitalia of *C. cerata*, *C. tremula*, and *C. sericea*: the saccus of each tapers to an acute apex, the aedoeagus of each possesses large cornuti, and none of these three species has large free lobes of the sacculus. *Chaetaglaea fergusonii* appears to be rarely encountered; it has been collected at both ultraviolet light traps and fermenting

fruit bait. Apparently univoltine, its winter flight period is influenced by temperature and other factors. The flight periods of *C. fergusonii*, *C. tremula* and *C. sericea* at one location in Louisiana are shown in Fig. 3.

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LARVAL HOSTS OF *URESIPHITA* HÜBNER (CRAMBIDAE)

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ABSTRACT. A survey of the literature and museum collections of *Uresiphita* indicates larval hosts are primarily quinolizidine-bearing plants in tribes of the Fabaceae. Three species, *Uresiphita reversalis*, *U. ornithopteralis* and *U. polygonalis*, were collected from seven genera in the Genisteae (*Chamaecytisus*, *Genista*, *Lupinus*, *Spartium*, *Laburnum*, *Ulex* and *Cytisus*) and from three genera in the Sophoreae (*Sophora*, *Pericopsis* and *Bolusanthus*). Two species, *U. reversalis* and *U. polygonalis*, were collected from three genera in the Thermopsidae (*Baptisia*, *Anagyris* and *Piptanthus*) and two, *U. reversalis* and *U. ornithopteralis*, were collected from two genera in the Bossiaceae (*Hovea* and *Templetonia*). A few legume species that are not known to bear quinolizidine alkaloids were also reported. In particular, *U. reversalis*, *U. polygonalis*, and *U. ornithopteralis* were each collected from *Acacia* (Mimosaceae) in areas as widely distributed as Australia and the United States (California, Texas and Hawaii). This is a consistent anomaly in the overall host-use pattern. Other nonleguminous species have been reported but are probably not indicative of hosts upon which development may be completed.

Additional key words: Pyralidae, Pyraustinae, aposematism, host plant range, French broom, quinolizidine alkaloids.

In 1983, *Uresiphita reversalis* (Guenée) caused significant damage to *Genista monspessulana* (L.) L. Johnson, also known as French broom, in the San Francisco Bay Area. Thus, *U. reversalis* was thought to be useful as a control agent against the introduced weedy brooms in California (Leen 1992, 1995). Little was known about the biology and host plant range of the genus *Uresiphita* Hübner so this survey of collections and publications was begun to ascertain if a pattern of host use could be detected.

Although the genus is in need of taxonomic revision, several species and subspecies are recognized and accepted as follows. *Uresiphita reversalis*, the *Genista* caterpillar, is the only species known to occur in North America (Munroe 1976). *Uresiphita ornithopteralis* Guenée, the tree-lucerne moth, is an Australian species (Common 1990). Several subspecies are recognized within *Uresiphita polygonalis* ([Denis and Schiffmüller]) by Clarke (1971). *Uresiphita polygonalis maoralis* (Felder & Rogenhofer), the kowhai moth, is indigenous to New Zealand; *Uresiphita polygonalis virescens* (Butler) is considered indigenous to Hawaii but may be introduced (Zimmerman 1958); and *Uresiphita polygonalis ochrocrossa* Clarke is indigenous to Rapa Island (Clarke 1971). Palm (1986) lists *Uresiphita limbalis* as a synonym of *U. polygonalis*. This paper presents a collation of information available on geographical distribution and hosts of these three species of *Uresiphita*.

MATERIALS AND METHODS

Information on the distribution and collections of *Uresiphita* was obtained from publications and museum collections. A list of these sources appears in Tables 1 and 2. The primary source of information on the dis-

TABLE 1. Published records and collections of leguminous host plants of *Uresiphita* spp. Sources: 1, Anonymous 1935; 2, Arnett 1985; 3, Calif. Acad. Sci., USA; 4, Calif. Dept. Food and Agric., USA; 5, Common 1990; 6, Crosswhite 1985; 7, Fenemore 1982; 8, Forbes 1923; 9, Froggatt 1907; 10, Gaslin 1966; 11, Gibbs 1976; 12, Hanneman 1964; 13, Hudson 1928; 14, Khotko and Molchanova 1974; 15, Kimball 1965; 16, Leonard 1926; 17, Los Angeles Co. Mus., USA; 18, Mastro 1990; 19, McKenzie 1933; 20, Meyrick 1889; 21, Miller 1935; 22, Mulvey 1978; 23, Munroe 1976; 24, Natl. Mus. Nat. Hist., Smithsonian Inst., USA; 25, Natural Hist. Mus., UK; 26, Perez de Paz et al. 1986; 27, personal collection; 28, Pinhey 1975; 29, Purdie 1882; 30, Scott 1984; 31, Smith 1890; 32, Swezey 1954; 33, Univ. Calif. Berkeley, USA; 34, Univ. Calif. Riverside, USA; 35, Univ. Missouri Columbia, USA; 36, Zimmerman 1958; 37, probably *Prosopis pallida* (Humb. & Bonpl. ex Willd.) Kunth.

Hostplant	<i>U. reversalis</i>	<i>U. polygonalis</i> (excl. <i>majoralis</i>)	<i>U. polygonalis</i> <i>majoralis</i>	<i>U. ornithopteralis</i>
CAESALPINIACEAE				
Cassiaceae				
<i>Cassia</i> L.	Florida ¹⁵			
<i>Cassia alata</i> L.	California ⁴			
FABACEAE				
Bossiceae				
<i>Hovea</i> R.Br ex W.T.Ait.				Australia ⁵
<i>Templetonia</i> R.Br. ex W.T.Ait.				Australia ^{5,9}
<i>Templetonia retusa</i> (Vent.) R.Br.	California ⁴		New Zealand ¹³	
Carmichaeliaceae				
<i>Carmichaelia</i> R.Br.				
Genisteae				
<i>Chamaecytisus profliferus</i> (L.) Link				Australia ^{5,9}
<i>Cytisus</i> Desf.	California ^{3,4} USA ²⁴	Germany ¹² Norfolk Island ²⁵ South Africa ²⁸	New Zealand ¹³	
<i>Cytisus scoparius</i> (L.) Link	California ³³			
<i>Cytisus supranubius</i> (L.) Kuntze	California ^{3,4,17} USA ²⁴			
<i>Genista</i> L.	California ^{3,4,5,6,18,24,33} Arizona ⁶ USA ²³	Germany ¹² USSR ¹⁴		Australia ⁵
<i>Genista linifolia</i> L.	California ¹⁸			

TABLE I. (continued)

Hostplant	<i>U. reversalis</i>	<i>U. polygonalis</i> (excl. <i>matroidalis</i>)	<i>U. polygonalis</i> <i>matroidalis</i>	<i>U. ornithopteridis</i>
<i>Genista monspessulana</i> (L.) L. Johnson	California ^{4,19} USA ²⁴			
<i>Genista stenopetalata</i> Webb & Berth.	California ⁴	Canary Islands ^{25,26}		
<i>Laburnum</i> Fabr.	California ⁴ Kansas ⁶ Nebraska ⁶ Maryland ⁶ USA ²⁴			
<i>Laburnum alpinum</i> (Mill.)	California ³³ USA ²⁴			
<i>Laburnum</i> x <i>watereri</i> "Vossii" (Kirchn.) Dipp.	California ²⁴			
<i>Lupinus</i> L.	Florida ¹⁵ California ^{4,33,34} New York ⁶ Texas ⁶ USA ^{23,24,35}	South Africa ²⁸	New Zealand ^{7,10,21,30,31}	Australia ⁵
<i>Lupinus arboreus</i> Sims	California ²⁷		New Zealand ^{1,22}	
<i>Lupinus diffusus</i> Nutt.	Florida ^{15,27}			
<i>Spartium junceum</i> L.	California ³ Georgia ⁶ USA ^{23,24}	South Africa ²⁸		Australia ⁵
<i>Ulex</i> L.				
<i>Ulex europaeus</i> L.		Germany ¹² Madeira ²⁵		
Phaseoleae				
<i>Phaseolus</i> L.		Germany ¹²		
Sophoreae				
<i>Bolusanthus</i> Harms		South Africa ²⁸		
<i>Pericopsis</i> Thwaites		South Africa ²⁸		
<i>Sophora</i> L.		Hawaii ³²	New Zealand ^{7,11,20}	
<i>Sophora arizonica</i> S. Wats.	USA ²⁴			
<i>Sophora chrysophylla</i> (Salisb.) Seem.	Arizona ⁶	Hawaii ³⁶		

TABLE I. (continued)

Hostplant	<i>U. reversalis</i>	<i>U. polygonalis</i> (excl. <i>matroidalis</i>)	<i>U. polygonalis</i> <i>matroidalis</i>	<i>U. ornithopteralis</i>
<i>Sophora microphylla</i> Ait. <i>Sophora secundiflora</i> (Ort.) Lag. ex DC	Arizona ^{6,23,24} Texas ⁶ USA ^{23,24}			Australia ⁵
<i>Sophora tetraptera</i> J.F.Mill. <i>Sophora tomentosa</i> L.	Florida ¹⁵ USA ²³	Northwest India ²⁵	New Zealand ^{10,29}	
Thermopsidae <i>Anagyris foetida</i> L. <i>Baptisia</i> Vent.	New York ^{8,16} USA ^{2,24} Florida ¹⁵ USA ^{23,24}	Spain ²⁵		
<i>Baptisia tinctoria</i> (L.) R.Br.	California ³	England ^{12,25}		
<i>Piptanthus</i> Sweet <i>Piptanthus nepalensis</i> (Hook.) D. Don ex Sweet Trifolieae <i>Trifolium</i> L. <i>Trifolium repens</i> L.			New Zealand ^{10,13} New Zealand ¹³	
MIMOSACEAE Acacieae <i>Acacia</i> Mill.	California ⁴ Texas ⁶ USA ²⁴			Australia ⁵
<i>Acacia koa</i> A. Gray Adenthereae honey locust ³⁷ Ingeae <i>Cedrela</i> P.Br.	California ⁴	Hawaii ³⁶		
		South Africa ²⁸		

tribution of species other than *U. reversalis* was the Natural History Museum, London, U.K. Very few host records were associated with those specimens, so the majority of host information for all *Uresiphita* species was obtained from the literature and correspondence or visits to museums and collections within the United States. Plant species' names are reported as they are currently accepted rather than exactly as reported on the records. Scientific names, in lieu of common names, are reported if no other species or genus could be accorded the common names of the associated collection record.

RESULTS

Distribution. The genus *Uresiphita* has been collected from all major continents occurring between 50° north and 50° south latitude. Collection sites in the northern hemisphere extend into parts of Canada (Nova Scotia), the southern part of the United Kingdom and into parts of Germany, Poland and the former USSR. Collection sites in the southern hemisphere extend to New Zealand, South Africa, and the Amazonian region of Brazil. Collections have also been made from parts of western China and several island locations, including Fiji, Norfolk Island, Rapa Island, the Hawaiian Islands, Madeira, the Canary Islands, the Bahamas and San Domingo. Munroe (1976) reported that *Uresiphita* is found in the Marquesas, although Clarke (1986) made no mention of this genus in his volume on the Pyralidae and Microlepidoptera of the Marquesas Archipelago. Munroe (pers. comm.) states this was an error on his part.

Hostplant relationships. Publications and collections of *Uresiphita* indicate all use leguminous species from tribes that are known to contain quinolizidine alkaloids (Table 1). These tribes are all within the Fabaceae and include the Genisteae, Thermopsidae, Sophoreae and Bossiaceae. Three species, *U. reversalis*, *U. ornithopteralis*, and *U. polygonalis*, were recorded from seven genera in the Genisteae (*Chamaecytisus*, *Genista*, *Lupinus*, *Spartium*, *Laburnum*, *Ulex* and *Cytisus*) and from three genera in the Sophoreae (*Sophora*, *Pericopsis* and *Bolusanthus*). Two species, *U. reversalis* and *U. polygonalis*, were recorded from three genera in the Thermopsidae (*Baptisia*, *Anagyris* and *Piptanthus*) and two, *U. reversalis* and *U. ornithopteralis*, were recorded from two genera in the Bossiaceae (*Hovea* and *Templetonia*). Other reported host tribes within the Fabaceae include the Phaseoleae (*Phaseolus*), Trifolieae (*Trifolium*) and the Carmichaeliae (*Carmichaelia*) (Table 1). The latter fabaceous tribes are not known to contain quinolizidine alkaloids.

Native host plants of *U. reversalis* include *Lupinus*, *Baptisia* and *Sophora* and introduced hosts include *Genista* and *Spartium* (Table 1). *Cytisus scoparius* (L.) Link is an introduced plant that is also reported

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Hostplant	<i>U. reversalis</i>	<i>U. polygonalis</i> (excl. <i>matralis</i>)	<i>U. polygonalis matralis</i>	<i>U. ornithopteralis</i>
Asteraceae				
<i>Chrysanthemum</i> L.				
Boraginaceae				
<i>Ehretia anacua</i> (Teran & Berl.) I.M. Johnston				
Buddleiaceae				
<i>Buddleja</i> L.				
Celastraceae				
<i>Putterlickia</i> Endl.				
Caprifoliaceae				
<i>Lonicera</i> L.				
<i>Lonicera sempervirens</i> L.				
<i>Viburnum</i> L.				
Geraniaceae				
<i>Pelargonium</i> L'Her.				
Liliaceae				
<i>Asparagus</i> L.				
Myrtaceae				
<i>Myrcia tomentosa</i> (Aubl.) DC				
Oleaceae				
<i>Olea europaea</i> L.				
<i>Forsythia</i> Vahl				
Rhamnaceae				
<i>Discaria toumatou</i> Raoul				
Rosaceae				
<i>Adenostoma fasciculatum</i> Hook. & Arn.				
<i>Rosa</i> L.				
Rutaceae				
<i>Citrus</i> L.				
Salicaceae				
<i>Salix</i> L.				
Ulmaceae				
<i>Ulmus</i> L.				
family undeterminable ¹⁴				

as a host of *U. reversalis* but these are not credible records (Leen 1992, 1997). Reported hosts of *U. reversalis* show a consistent geographic pattern in the USA. *Lupinus* spp. are the most widespread native hosts; *Baptisia* spp. are hosts in the east, central and south, and *Sophora* spp. are hosts along parts of the south, especially desert areas such as Texas and Arizona. In the west, *Lupinus* is the only reported native host genus with the earliest record dating from 1930 in Riverside, California. Introduced plants in the genera *Genista*, *Spartium*, *Cytisus*, *Laburnum*, *Piptanthus* and *Templetonia* are reported as hosts throughout the USA. These introduced plants are particularly abundant along the western regions and thus are more frequently reported as hosts of *U. reversalis* than are the relatively less abundant, perennial species of *Lupinus*.

The other two families of legumes, Mimosaceae and Caesalpinaceae, are reportedly used by one or more species of *Uresiphita* (Table 1). *Uresiphita reversalis* was collected from *Cassia* spp. in the Caesalpinaceae (Cassieae) in both California and Florida. Collections of *U. reversalis* from the Mimosaceae are in three tribes: the Ingeae, the Adenthereae, and the Acacieae. Species of *Acacia* (Acacieae) are reported as hosts of *U. reversalis*, *U. polygonalis* and *U. ornithopteralis*. Collections of *U. reversalis* are from *Acacia* in both California and Texas. *Uresiphita polygonalis* were collected from *Acacia koa* A. Gray in Hawaii, and *U. ornithopteralis* were collected from an *Acacia* sp. in Australia.

Other records include nonleguminous families (Table 2). *Uresiphita polygonalis* was reported from *Putterlickia* in the South African family Celastraceae. *Uresiphita polygonalis maorialis* was collected from *Discaria* (Rhamnaceae) and *Chrysanthemum* (Asteraceae) in New Zealand. And *U. ornithopteralis* caused heavy damage to willows (*Salix*) in Australia. Collections and publications of *U. reversalis* were from 10 to 11 nonleguminous families, including the Boraginaceae, Buddleiaceae, Caprifoliaceae, Geraniaceae, Liliaceae, Myrtaceae, Oleaceae, Rosaceae, Rutaceae, Ulmaceae and either the Lauraceae, Myricaceae, or Ericaceae. Two or three species are from plants in each of the Caprifoliaceae, Oleaceae and Rosaceae. All other families were reported on only one occasion. Powell (1992) reported two additional families (Taxaceae and Rubiaceae) as possible hosts that I have not included in my collation for the following reasons. Both records are from the California Department of Food and Agriculture collections. Only pupae were collected from *Taxus* (Taxaceae) and the record or specimen of the collection from *Gardenia* (Rubiaceae) could not be located. Data from Powell's paper were not tabulated since they duplicate information presented here and include some questionable data from Bernays and Montllor (1989). Host specificity tests on *U. reversalis* are presented in Leen (1997) and clarify this matter.

Uresiphita reversalis was collected in California on three separate occasions from barbecue covers originating in Connecticut, Vermont and Massachusetts (California Department of Food and Agriculture Records). The three collections from barbecue covers exceed the number of times larvae were collected from most nonleguminous plants and, obviously, barbecue covers are a 'host' upon which development is not completed.

DISCUSSION

In general, the larval host plants of the genus *Uresiphita* are confined to the quinolizidine-bearing tribes of the Fabaceae. This suggests quinolizidine alkaloids are important to the determination of the host range of *Uresiphita*. The sequestering of quinolizidine alkaloids from *G. monspesulana* by *U. reversalis* was confirmed by Bernays and Montllor (1989) and Montllor et al. (1990). Other *Uresiphita* species also may be found to sequester quinolizidine alkaloids since the aposematic coloration, gregarious habits and host plant range are similar among *Uresiphita* larvae (Leen 1992, 1995). One genus, *Cytisus*, bears quinolizidine alkaloids but is not suitable for development of both *U. reversalis* and *U. polygonalis* (Leen 1992, 1997). Confusion in nomenclature has surely led to erroneous reports on *Cytisus* and thus all reports remain to be substantiated (Leen 1992, 1997). Collections from other genera in tribes of the Fabaceae and from the Caesalpiniaceae are questionable because members of these tribes were rejected by *Uresiphita* and collections are rare. However, the collections of three species of *Uresiphita* from *Acacia* spp. in different localities suggest this may be an accurate report. This is an anomalous host plant since *Acacia* is not known to bear quinolizidine alkaloids although *Acacia* has been reported to contain other types of alkaloids (White 1954, 1957).

Although some nonleguminous plant families are known to contain genera that bear quinolizidine alkaloids (Schwartz 1973, Wink 1992), none of the tested genera in these particular families and others were acceptable (Leen 1997). Just as the collections from barbecue covers are not indicative of host use, most of these collection records are probably not indicative of species used by *Uresiphita*. A few other important facts help to discredit these collections as true hosts. Mulvey (1978) noted the collection of *U. p. maoralis* from *Chrysanthemum* occurred because larvae had migrated from their original host, *Lupinus*. *Lonicera sempervirens*, honeysuckle, is frequently cited as a host plant of *U. reversalis*. *Hedysarum coronarium* L. is known as French honeysuckle. French honeysuckle may have been a collection host, and the common names may have led to confusion. However, both species were rejected in the lab and are probably not acceptable hosts under field conditions.

Species in the Genisteae, Sophoreae, Thermopsidae and Bossiaceae

are undoubtedly hosts of *Uresiphita* spp. Further research in regard to genera such as *Acacia* may refute the present conclusions.

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HOST SPECIFICITY OF *URESIPHITA REVERSALIS* (GUENÉE) (CRAMBIDAE)

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ABSTRACT. Host specificity tests were conducted on *Uresiphita reversalis* and to a lesser degree on *U. polygonalis*. First instars of *U. reversalis* were limited to feeding on quinolizidine-bearing tribes of fabaceous legumes. However, *U. polygonalis* from the Canary Islands and *U. reversalis* both failed to complete development on *Cytisus scoparius* (Genisteae) beyond the second instar. *Cytisus scoparius* and *Cytisus striatus* were never observed as hosts of *U. reversalis* in California during the years of this study (1984–1989). Host range of *U. reversalis* encompassed six quinolizidine-bearing tribes of the Fabaceae: Genisteae, Sophoreae, Thermopsidae, Bossiaceae, Podalyreae, and Euchrestae, although the latter two tribes have not been reported as hosts in the field. Both native and introduced species in quinolizidine-bearing tribes will undoubtedly be used by *U. reversalis* when the opportunity arises.

Additional key words: Pyralidae, Pyraustinae, aposematism, host plant range, French broom, quinolizidine alkaloids.

Uresiphita reversalis (Guenée) expanded its host range from native legumes to include several introduced ornamental broom species. Feeding by *U. reversalis* on *Genista monspessulana* (L.) L. Johnson (commonly known as French broom or Genista) was first reported to the USDA Agricultural Research Service, Albany, California, in 1983 when larvae caused substantial defoliation of some populations in the San Francisco Bay area. These studies were undertaken to determine if *U. reversalis* might be used to control the introduced weedy brooms in California (Leen 1992). Unfortunately, plants defoliated in the summer or fall were completely refoliated the following spring. Early spring growth of the brooms prior to the increase of insect populations also indicated *U. reversalis* was unlikely to be a significant control agent. Studies on the potential host range of *U. reversalis* were completed even though the insect was no longer considered a potential, augmentative control agent.

MATERIALS AND METHODS

Host acceptance tests of first instars of *U. reversalis* were conducted on insects originating from Alameda County, California, USA and *U. polygonalis* (Denis & Schiffermüller) originating from Masca, Tenerife, Canary Islands, Spain. *Uresiphita reversalis* was collected from *G. monspessulana*, and *U. polygonalis* was collected from *Retama monosperma* (L.) Boiss. First instars were obtained by collecting and rearing larvae to adults and later removing newly laid eggs from foliage before hatching. Upon hatching, one or two, and occasionally more, larvae were placed on each test plant. An equal number of larvae was used as controls and

TABLE 1. Plants in the Fabaceae accepted by first instars of *Uresiphita reversalis*. P = potted plant tested, C = cutting (excised leaf) tested.

Hostplant	No. insects	No. plants	P/C
Genisteae			
<i>Cytisus scoparius</i> (L.) Link	20	20	P
<i>Cytisus scoparius</i> (Dallimore hybrid) (lilac broom)	10	10	P
<i>Cytisus striatus</i> (Hill) Rothm.	20	20	C
<i>Genista lydia</i> Boiss.	12	6	P
<i>Genista linifolia</i> L.	30	30	P
<i>Genista monspessulana</i> (L.) L. Johnson	30	30	P
<i>Genista tinctoria</i> L.	24	24	P
<i>Genista stenopetala</i> Webb & Berth.	32	32	P
<i>Laburnum anagyroides</i> Medik.	26	26	P
<i>Laburnum alpinum</i> (Mill.) Ber. & J.Presl.	30	30	P
<i>Lupinus albifrons</i> Benth.	30	30	C
<i>Lupinus arboreus</i> Sims	30	30	P
<i>Lupinus chamissonis</i> Eschsch.	30	30	P
<i>Lupinus luteus</i> L.	20	20	P
<i>Lupinus succulentus</i> Koch	20	20	P
<i>Lupinus variicolor</i> Steudel	20	10	C
<i>Spartium junceum</i> L.	25	25	P
<i>Ulex europaeus</i> L.	20	20	P
Thermopsidae			
<i>Baptisia australis</i> (L.) R.Br.	30	30	P
<i>Baptisia lactea</i> (Raf.) Thieret.	30	30	P
<i>Baptisia tinctoria</i> (L.) Vent.	30	30	P
<i>Thermopsis rhombifolia</i> Nutt. ex Richards.	30	15	P
<i>Thermopsis macrophylla</i> Hook. & Arn.	30	15	C
Sophoreae			
<i>Sophora davidii</i> (Franch.) Skeels.	6	3	P
<i>Sophora secundiflora</i> (Ort.) Lag. ex DC	30	30	P
Podalyreae			
<i>Podalyria sericea</i> (Andrews) R.Br.	8	4	P
Euchrestae			
<i>Euchresta</i> Benn.	4	2	P
Vicieae			
<i>Vicia sativa</i> L. (flowers only)	16	40	C

placed on *G. monspessulana* cuttings. Development was observed until the first instar was completed. Later, tests of *U. reversalis* and *U. polygonalis* on *Cytisus scoparius* (L.) Link were continued beyond the first instar to determine if development could be completed on this species. All experiments were conducted on naive larvae under a 16L:8D photoperiod at 20° C. Developmental tests were conducted on *C. scoparius* because *U. reversalis* was observed under field conditions to oviposit and complete development through the fifth instar on almost all other

TABLE 2. Leguminous plants rejected by *Uresiphita reversalis* larvae. P = potted plant tested, C = cutting (excised leaf) tested.

Hostplant	No. insects	No. plants	P/C	Instar
Fabaceae				
Genisteae				
<i>Cytisus scoparius</i> (L.) Link	20	20	C	2
Thermopsidae				
<i>Pickeringia montana</i> Nutt.	41	11	C	1
Hedysareae				
<i>Hedysarum coronarium</i> L.	30	30	P	1
<i>Lepedeza bicolor</i> Turcz.	8	4	P	1
Trifolieae				
<i>Ononis</i> L.	30	30	P	1
<i>Medicago sativa</i> L.	26	26	P	1
<i>Trifolium</i> L.	26	26	P	1
Loteae				
<i>Anthyllis vulneraria</i> L.	30	30	P	1
<i>Lotus scoparius</i> (Nutt.) Ottley	25	25	P	1
Vicieae				
<i>Lathyrus latifolius</i> L.	24	12	P	1
<i>Vicia villosa</i> Roth	9	25	C	1
Desmodieae				
<i>Indigofera tinctoria</i> L.	16	8	P	1
Phaseoleae				
<i>Pueraria lobata</i> (Willd.) Ohwi.	6	3	P	1
Crotalarieae				
<i>Crotalaria capensis</i> Jacq.	8	4	P	1
Caesalpinjiaceae				
Cercidae				
<i>Cercis canadensis</i> L.	20	10	P	1
<i>Cercidium floridum</i> A. Gray	16	8	P	1
Cassieae				
<i>Ceratonia siliqua</i> L.	6	3	P	1
Mimosaceae				
Ingeae				
<i>Albizia julibrissin</i> Durazz.	8	4	P	1
Mimoseae				
<i>Mimosa pudica</i> L.	16	8	P	1
<i>Leucaena leucocephala</i> (Lam.) DeWit	20	10	P	1
Acacieae				
<i>Acacia</i> Mill.	10	10	P	1
<i>Acacia longifolia</i> (Andrews) Willd.	2	6	C	1

reported hosts in the Genisteae except *C. scoparius* and *Cytisus striatus* (Hill) Rothm. Again, an equal number of larvae were used as controls and placed on *G. monspessulana*. The plant species used in tests of *U. reversalis* are listed in Tables 1 and 2. First instars of *U. polygonalis* were tested on potted plants of *Phaseolus vulgaris* L., and an equal number of larvae were tested on *G. monspessulana*.

Fourth instars of *U. reversalis* from Alameda County, California, were

tested on *Lonicera sempervirens* L., *Convolvulus arvensis* L., and *Eugenia* L. sp. Fourth instars of *U. reversalis* originating from a population near Lake Placid, Florida, and collected from *Lupinus diffusus* Nutt., were also tested on cuttings of *L. sempervirens*. In each test, one larva was tested on each plant and an equal number of larvae were tested on *G. monspessulana*. Both populations were fed *G. monspessulana* prior to testing and observed under the same environmental conditions as above.

Nearly all potted plant specimens were originally collected as seed from locations within California or obtained from a variety of commercial seed sources and botanical gardens within the USA and abroad. The Botanical Garden at the University of California, Berkeley, graciously provided many of the seeds from sources outside California. Plants grown from seed were fertilized biweekly for the first three months on Hoagland's solution (Hoagland & Arnon 1938). Older plants were then fertilized every six to nine months with a timed-release, 17-6-10, fertilizer (Osmocote). Attempts were made to infect test plants with *Rhizobia* by inoculating soil with roots infected with *Rhizobia* from closely related plants. A few of the potted plants were obtained by purchasing mature plants from nurseries. These potted plants were fertilized with Osmocote as above. Tests with cuttings were conducted on plant specimens obtained from localities within California and initiated within 48 hours from the time of collection.

RESULTS

First instars of *U. reversalis* from California accepted 27 plant species from five tribes (Genisteae, Thermopsidae, Sophoreae, Podalyreae, and Euchrestae) in the Fabaceae (Table 1). All accepted tribes are well represented by species bearing quinolizidine alkaloids (Wink 1992) with a few exceptions. *Pickeringia montana* Nutt., in the Thermopsidae, is not known to contain quinolizidine alkaloids and was rejected by *U. reversalis* (Table 2). Flowers, but not leaves, of *Vicia sativa* L. in the Viciaeae were accepted by *U. reversalis*. Neither this species nor the tribe are reported to contain quinolizidine alkaloids. The foliage of *V. sativa* and the foliage and flowers of *Vicia villosa* were both unacceptable to *U. reversalis* (Table 2).

Fourteen species from eight tribes (Thermopsidae, Hedysareae, Trifolieae, Loteae, Viciaeae, Desmodieae, Phaseoleae and Crotalarieae) in the Fabaceae were rejected by first instars of *U. reversalis* (Table 2). Eight species from five tribes of nonfabaceous legumes were also rejected by first instars (Table 3). Thirty two species in 12 nonleguminous families were rejected by first instars, and three species in three families were rejected by fourth instars (Table 2.) Some of these rejected families (e.g., Ranunculaceae, Scrophulariaceae) were chosen for testing be-

TABLE 3. Non-leguminous plants rejected by *Uresiphita reversalis* larvae. P = potted plant tested, C = cutting (excised leaf) tested.

Hostplant	No. insects	No. plants	P/C	Instar
Caprifoliaceae				
<i>Lonicera japonica</i> Thumb.	19	4	P	1
<i>Lonicera hispidula</i> Dougl.	45	5	P	1
<i>Lonicera sempervirens</i> L.	40	20	P	1
<i>Lonicera sempervirens</i> L.	15	15	P	4
<i>Sambucus mexicana</i> C. Presl.	8	4	P	1
<i>Symphoricarpus albus</i> (L.) S.F. Blake	5	5	P	1
Asteraceae				
<i>Arctium minus</i> (Hill) Bernh.	24	24	P	1
<i>Calendula officinalis</i> L.	20	20	P	1
<i>Centaurea cyanus</i> L.	24	24	P	1
<i>Centaurea diffusa</i> Lam.	48	48	P	1
<i>Centaurea maculosa</i> Lam.	24	24	P	1
<i>Chrysanthemum leucanthemum</i> L.	30	30	P	1
<i>Chrysanthemum parthenium</i> (L.) Bernh.	30	30	P	1
<i>Helianthus tuberosus</i> L.	40	20	P	1
<i>Isatis tinctorius</i> L.	32	16	P	1
<i>Santolina chamaecyparissus</i> L.	19	5	P	1
<i>Serratula radiata</i> (Waldst. & Kit.) Bieb.	24	24	P	1
<i>Silene italica</i> (L.) Pers.	20	20	P	1
<i>Tagetes erecta</i> L.	8	4	P	1
Euphorbiaceae				
<i>Euphorbia esula</i> L.	20	20	P	1
Convolvulaceae				
<i>Convolvulus arvensis</i> L.	25	25	P	1
<i>Convolvulus arvensis</i> L.	20	20	P	4
Papaveraceae				
<i>Eschscholzia californica</i> Cham.	30	30	P	1
<i>Papaver orientale</i> L.	30	30	P	1
<i>Papaver somniferum</i> L.	46	46	P	1
Ranunculaceae				
<i>Cimicifuga racemosa</i> (L.) Nutt.	20	1	P	1
<i>Aconitum napellus</i> L.	20	1	P	1
Malvaceae				
<i>Malva alcea</i> L.	24	24	P	1
Scrophulariaceae				
<i>Antirrhinum majus</i> L.	20	20	P	1
Plantaginaceae				
<i>Plantago lanceolata</i> L.	24	24	P	1
Brassicaceae				
<i>Brassica oleracea</i> L.	20	20	P	1
Lamiaceae				
<i>Mentha aquatica</i> L.	24	24	P	1
Myrtaceae				
<i>Eugenia</i> L.	15	1	C	4
Boraginaceae				
<i>Ehretia anacua</i> (Teran & Berl.) I.M. Johnson	45	30	P	1

cause they are reported to contain species bearing quinolizidine alkaloids. Several of the rejected plant species (*L. sempervirens*, *Ehretia anacua* (Teran & Berl.) I. M. Johnston and *Eugenia*) were reported as hosts of *U. reversalis*.

Although *U. reversalis* completed development on *C. scoparius* and *C. striatus* through the first instar (Table 1), larvae did not complete development beyond the second instar on *C. scoparius* (Table 2). *Uresiphita polygonalis* did not complete development beyond the second instar on *C. scoparius* (n = 20 potted plants tested) or beyond the first instar on *P. vulgaris* (n = 22 potted plants tested). Fourth instars of *U. reversalis* from California did not feed upon nonleguminous plants (Table 3). All larvae died before molting or pupating. The Floridean population of *U. reversalis* also refused to accept *L. sempervirens* (n = 15 cuttings tested). Most of the rejected plants are not known to bear quinolizidine alkaloids. Control larvae rarely died or failed to complete development on *G. monspessulana*. Observed deaths were attributed to handling problems rather than to the control plants and are therefore not tabulated.

DISCUSSION

There are inconsistencies among reported hosts and host acceptance tests of *Uresiphita*. Although *C. scoparius* is a reported host for several species of *Uresiphita*, the accuracy of such reports is questionable for several reasons. First, rejection of *C. scoparius* by both *U. reversalis* and *U. polygonalis* indicates this species could not support these larvae through complete development. Second, *C. scoparius* is frequently confused with *G. monspessulana* by collectors in California. Insect specimens are thus labelled incorrectly with records of Scotch broom, *Cytisus* or *C. scoparius*, as the host plant. Third, *G. monspessulana* was classified as *Cytisus monspessulanus* L. in several floras. Inaccurate records for other species of *Uresiphita* in regard to *Cytisus* may also exist. The rejection of *C. scoparius* by *U. reversalis* and *U. polygonalis* does not exclude the possibility that other species of *Uresiphita* use *Cytisus* and are able to complete development. An explanation as to why *C. scoparius* is apparently the only rejected species in the tribe Genisteae cannot presently be offered. Tests on *C. striatus* were not conducted beyond the first instar for *U. reversalis* (Table 4). Larvae may be unable to complete development beyond the second instar on other species of *Cytisus*.

Bernays and Montllor (1989), citing my preliminary host plant data for first instars, reported that feeding does not occur upon *Pickeringia*, *Trifolium*, *Vicia*, and *Medicago* and that extensive feeding occurs on *C. scoparius*, *C. striatus*, *L. arboreus*, and *G. monspessulana*. They also stated that development cannot be completed upon *Laburnum* or *Ulex*.

Only the information on *L. arboreus*, *G. monspessulana*, *Pickeringia montana* (a monotypic genus), *Trifolium*, and *Medicago* is accurate.

Although some nonleguminous plant families are known to contain genera that bear quinolizidine alkaloids (Schwartz 1973, Wink 1992), none of the tested genera in these particular families and others were acceptable. Most of these collection records are probably not indicative of species used by *Uresiphita*.

Two genera (*Adenostoma*, *Rosa*) in the Rosaceae have been reported as hosts of *U. reversalis*. The collection and rearing of larvae from *Adenostoma fasciculatum* Hook. & Arn. was from a location where other probable hosts are not present (the old lighthouse at Point Loma, California) and thus is assumed accurate. First instars of *U. reversalis* did not complete development on *A. fasciculatum* in the lab. Two explanations are offered for the conflicting collection record and laboratory results. One, *A. fasciculatum* may be an acceptable host for later instars if *U. reversalis* was transferred (e.g., by humans) onto *Adenostoma*. Two, the source of test plants of *A. fasciculatum* was central California rather than southern California where the insect was collected. Host plant variation may explain the laboratory rejection of *A. fasciculatum*.

Larval hosts of *Uresiphita* spp. are primarily limited to quinolizidine-bearing tribes of the Fabaceae (Leen 1992 1997) and larval hosts of *U. reversalis* are similarly limited in range. Native hosts come from three tribes: Genisteae, Sophoreae, and Thermopsidae. However, host specificity tests, collections, and publications indicate additional species bearing these alkaloids will be utilized when the opportunity arises.

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DISTRIBUTION AND PHENOLOGIES OF LOUISIANA SPHINGIDAE

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ABSTRACT. The abundance, distribution, and flight periods for 55 species of Louisiana Sphingidae are presented, including prior literature records and new collecting data for 44 species taken over a 26-year period (1970 through 1995). Information is provided on the number of annual broods for 36 species, and dates of capture are plotted as one-year and composite graphs for 30 species.

Additional key words: bait traps, hawkmoths, light traps, sphinx moths, voltinism.

The first treatment of the family Sphingidae in Louisiana was presented by von Reizenstein (1863), who reported 33 species from the vicinity of New Orleans. Later, von Reizenstein (1881) and Ottolengui (1894) each tallied one additional species for the state, and subsequent published works during this century have gradually expanded the total by another dozen species (see Rothschild & Jordan 1903, Hine 1906, Clark 1917, Draudt 1931, Jung 1950, Merkl & Pfrimmer 1955, Pfrimmer 1957, Brou 1980, Covell 1984, Brou 1994). For some time, we have been monitoring and collecting adult Louisiana Sphingidae in order to produce a comprehensive state list and examine voltinism and variation in the abundance of adults from brood to brood. In the present paper, we discuss the results from 26 years of sampling, 1970 through 1995.

MATERIALS AND METHODS

We used ultraviolet light traps and fermenting bait traps to attract sphingids, logging approximately 416,000 light trap hours and 633,000 bait trap hours from 1970 through 1995. Occasional sampling was done using hand nets, flight traps, and pitfall traps. Many different light trap designs were used, but generally the traps employed lamps with adjacent baffles mounted over a funnel (see Brou 1992a, 1992b for details). Most of the lamps were black lights, ranging from 15 to 1000 watts, used singly, or in various combinations. Light traps varied from 60 to 3500 watts each, though most were in the 250 to 600 watt range. As many as six light traps were operated dusk to dawn, irrespective of climatic conditions, using photoelectric controls. Up to eight bait traps were operated year-round during 1984–1995.

Brood numbers were estimated by examining yearly graphs of capture totals plotted against sampling date for individual sphingid species. Ap-

proximately 2000 such graphs were prepared and studied, yielding data sufficient to estimate the number of annual broods for 36 species. Representative single-year graphs and composite-year graphs are presented in Figs. 3–52 (see Results and Species Accounts for discussion).

Specimens retained during this study are deposited at several institutional and private collections, the largest numbers of specimens being in the Florida State Collection of Arthropods (Gainesville), Louisiana State University (Baton Rouge) and in the collection of the senior author. Most specimens were from nine locations that were monitored on a frequent or continuous basis. These were, in decreasing order of sampling intensity: St. Tammany Parish, Sec. 24, T6, SR12E, 6.8 km NE Abita Springs; St. John the Baptist Parish, Edgard; Iberville Parish, Sunshine; Lafourche Parish, Cut Off; West Feliciana Parish, Sec. 63 and Sec. 76, T1S, R3W, 3.2 km NE Turnbull/Weyanoke; Ascension Parish, Prairieville; Tangipahoa Parish, Fluker; Natchitoches Parish, Kisatchie National Forest; Orleans Parish, New Orleans. Nomenclature follows Hodges (1983) with minor modifications.

RESULTS

General Trends. A total of 71,836 specimens of 55 species of Sphingidae was sampled from 43 of 64 Louisiana parishes (Fig. 1). Of the remaining 21 parishes, some were not visited, and a few yielded no Sphingidae. The greatest number of species (40) was recorded from St. Tammany Parish. Distribution maps for each of the 55 species are presented in Figs. 2.1–2.55, using data from our study supplemented by those few prior literature records for which accurate locality information could be determined.

Table 1 lists the monthly sampling totals from our study for each of the 55 species. Over 96 percent of the specimens came to light or bait during the period March to September. All 55 of the sphingid species that we sampled came to ultraviolet light traps (including *Hemaris thysbe* (F.), *H. diffinis* (Bdv.), and *Amphion floridensis* B. P. Clark). *Darapsa myron* (Cram.) was the most common species, accounting for over 26 percent of the total. Species more often taken in fermenting bait traps included *Sphinx kalmiae* Neum., *Enyo lugubris* (L.), *Sphecodina abbottii* (Swainson), *A. floridensis*, *D. myron*, and *Darapsa pholus* (Cram.) (Platt (1969) reported collecting some of these same species at fruit bait). Several specimens each of species not generally known to be attracted to fermenting bait were taken by this method, including *Laothoe juglandis* (J. E. Smith), *H. diffinis*, *Darapsa versicolor* (Harr.), and *Xylophones tersa* (L.). Several *Agrius cingulata* (F.) and *Amphion floridensis* were captured in pitfall traps baited with a mixture of feces, water, and ethylene glycol.

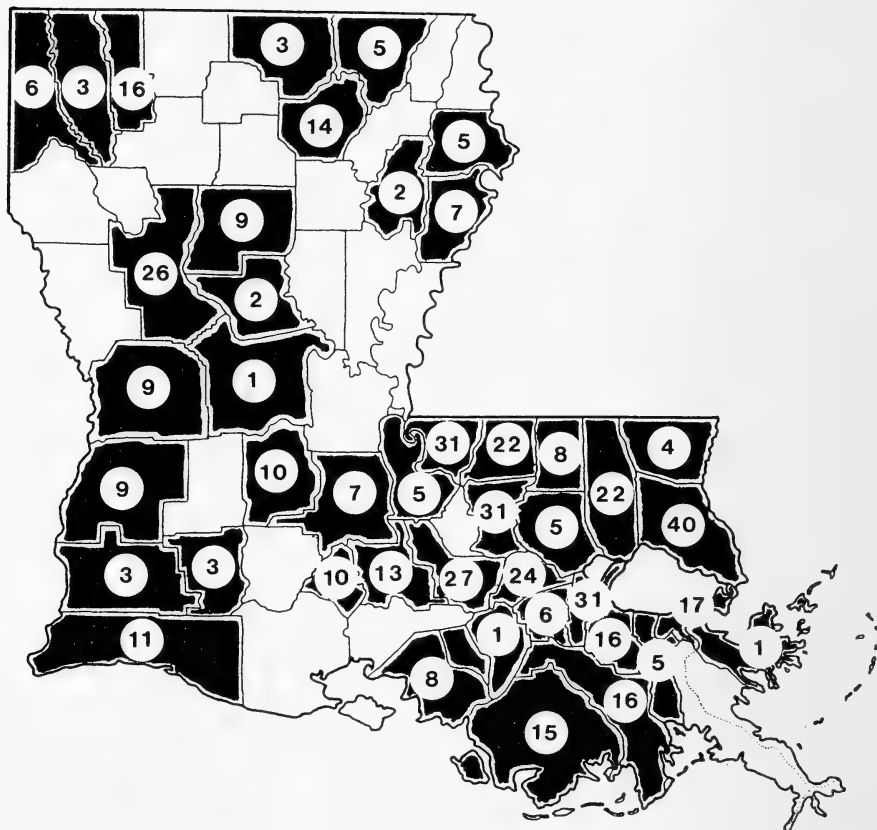
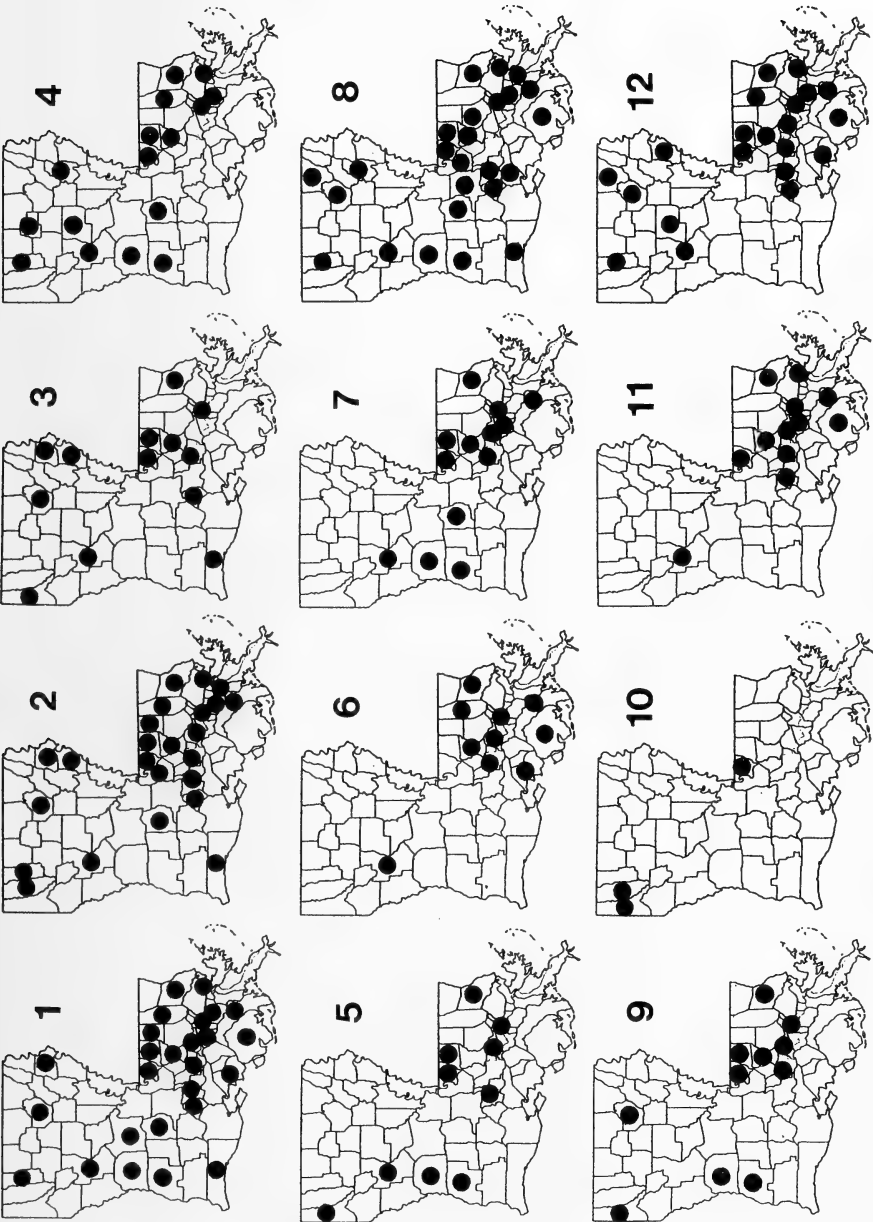
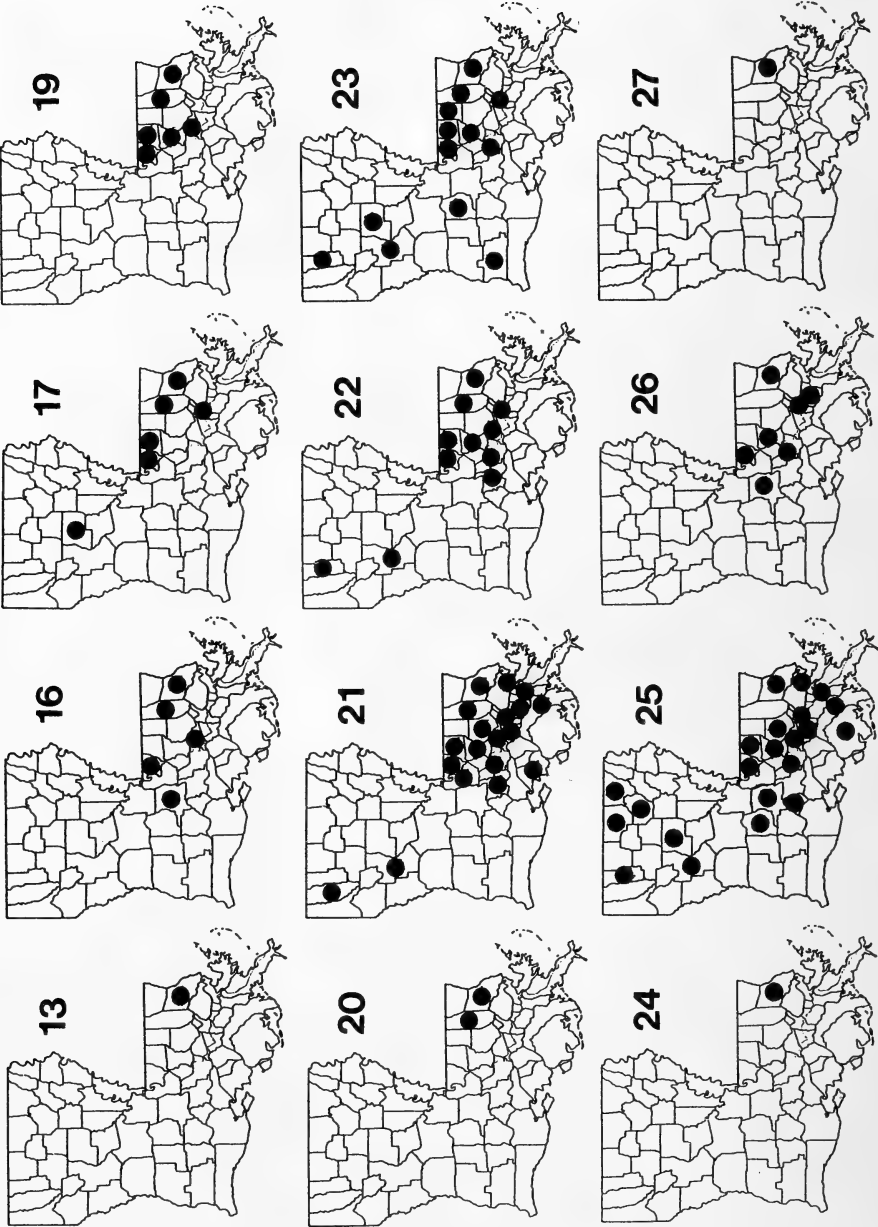


FIG. 1. Number of Sphingidae species recorded for each Louisiana parish, from sampling during 1970–1995.

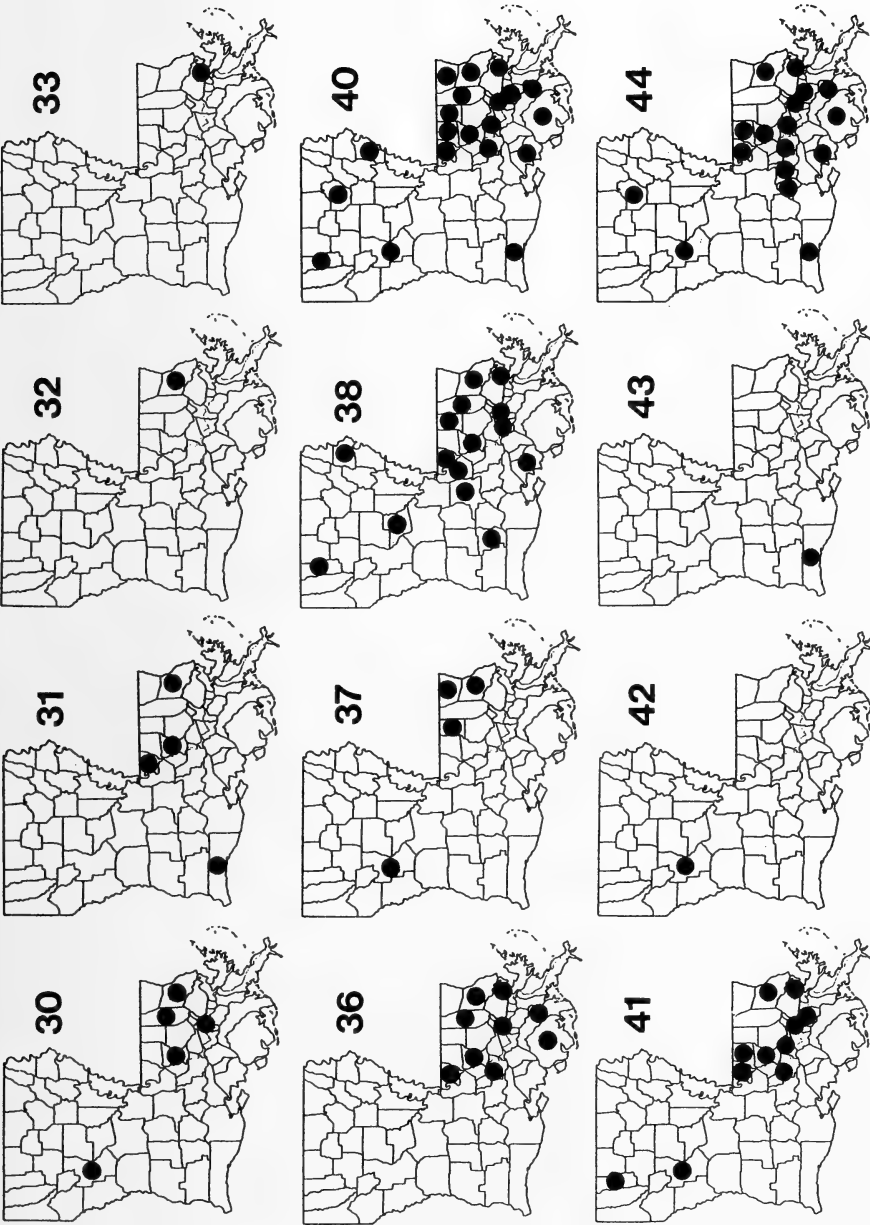
A total of 47 of the 55 species had been recorded previously from Louisiana, and 8 are reported here as new state records (B in Table 1). We failed to locate six species recorded by von Reizenstein (1863, 1881) (V in Table 1), two recorded by Jung (1950) (J in Table 1), and one recorded by Ottolengui (1894) (O in Table 1). We have been unable to locate specimens from the literature reports tabulated earlier, and Jung (pers. comm.) indicated that specimens taken during his investigation no longer exist. Two species, *Sphinx leucophaeta* Clem. and *Sphinx chersis* (Hbn.), reported by von Reizenstein (1863) seem questionable, although these species are known from one or more adjoining states. These records may actually refer to *Sphinx franckii* Neum., which was not recognized and named until 30 years after von Reizenstein's publication. Ottolengui's (1894) report of *Eumorphia licaon* (Cram.) likely was



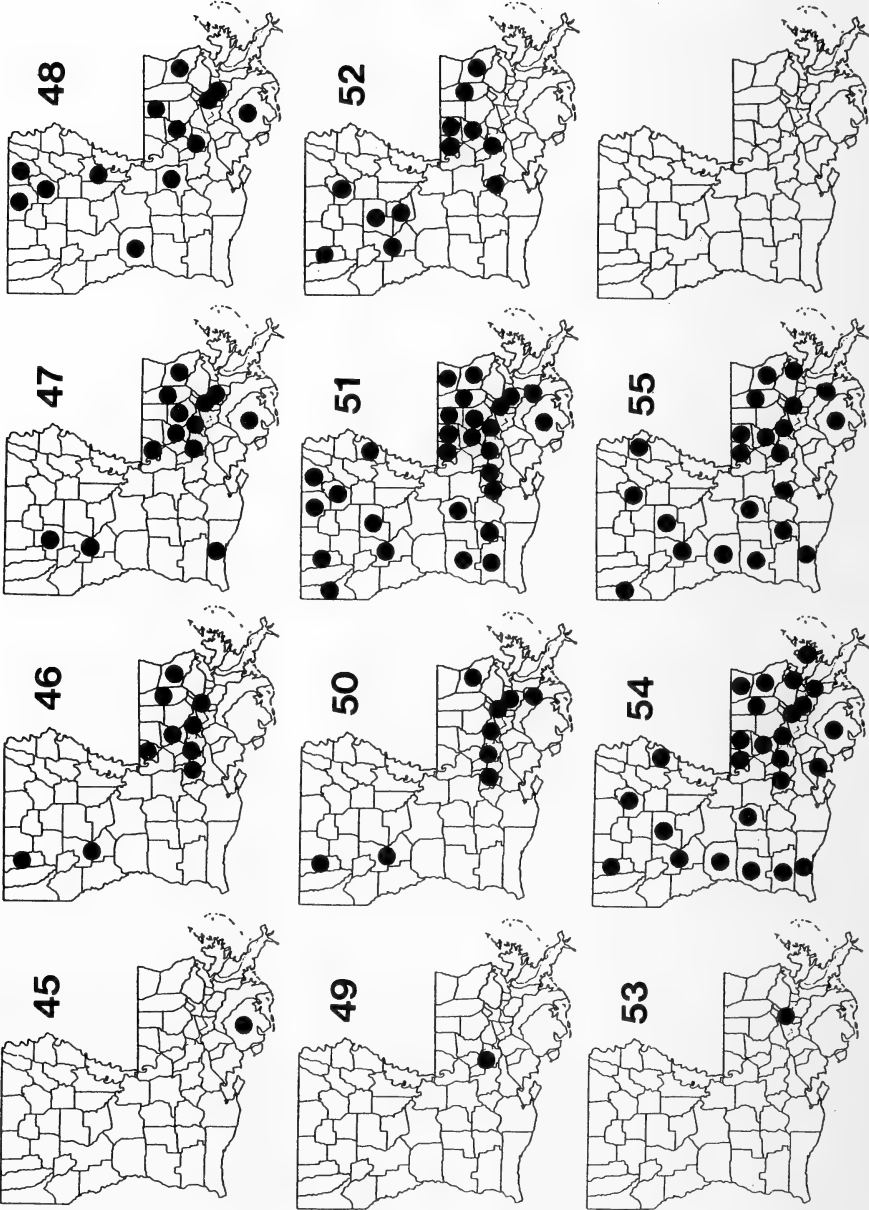
FIGS. 2.1-2.12. Distributions of Louisiana Spingidae. Map number corresponds to number for species in Table 1.



FIGS. 2.13-2.27. Distributions of Louisiana Sphingidae. Map number corresponds to number for species in Table 1.



FIGS. 2.30-2.44. Distributions of Louisiana Sphingidae. Map number corresponds to number for species in Table 1.



FIGS. 2.45-2.55. Distributions of Louisiana Spingidae. Map number corresponds to number for species in Table 1.

Eumorphia intermedia (B. P. Clark), a similar, smaller species, not described until 23 years later.

Among sphingid surveys from adjoining states, Freeman (1938) recorded 32 species from Arkansas, and only one of his species, *Sphinx gordius* Cramer, remains unrecorded from Louisiana (Riotte (1980) suggested that this record was probably *Sphinx poecila* Stephens). All the sphingids in the following three surveys are known from Louisiana: the 28 species listed by Selman and Barton (1971) from northeastern Arkansas; the 26 species listed by Neck (1991) from Walker County, Texas; and the 24 species listed by Taylor and Taylor (1965) from the Gulf Coast of Mississippi.

Annual Brood Patterns. We were able to estimate the number of annual broods in Louisiana for 36 of 55 species of Sphingidae (see Species Summaries). Nearly all of our findings differ from previously published sphingid voltinism in other states (e.g., Beutenmuller 1895, Hodges 1971, Covell 1984, Heitzman 1987), with Louisiana's southerly location generally promoting additional broods. For many of the multi-brooded species, the interval between the first brood peak and the second brood peak in any given year proved to be sometimes two times greater than the intervals between the remaining brood peaks; these subsequent intervals were usually consistent, or nearly so, throughout the remainder of the year. This initial nonconforming brood interval is of different duration depending on the species. The initial spring broods of some species can also be quite protracted, likely influenced at least in part by unpredictable spring climatic influences upon both the moths and their foodplants. The initial brood peaks varied by a month or more from one year to another. Variability in initial brood emergence appears to affect the timing of subsequent broods, but the magnitude of the effect differs in any given year.

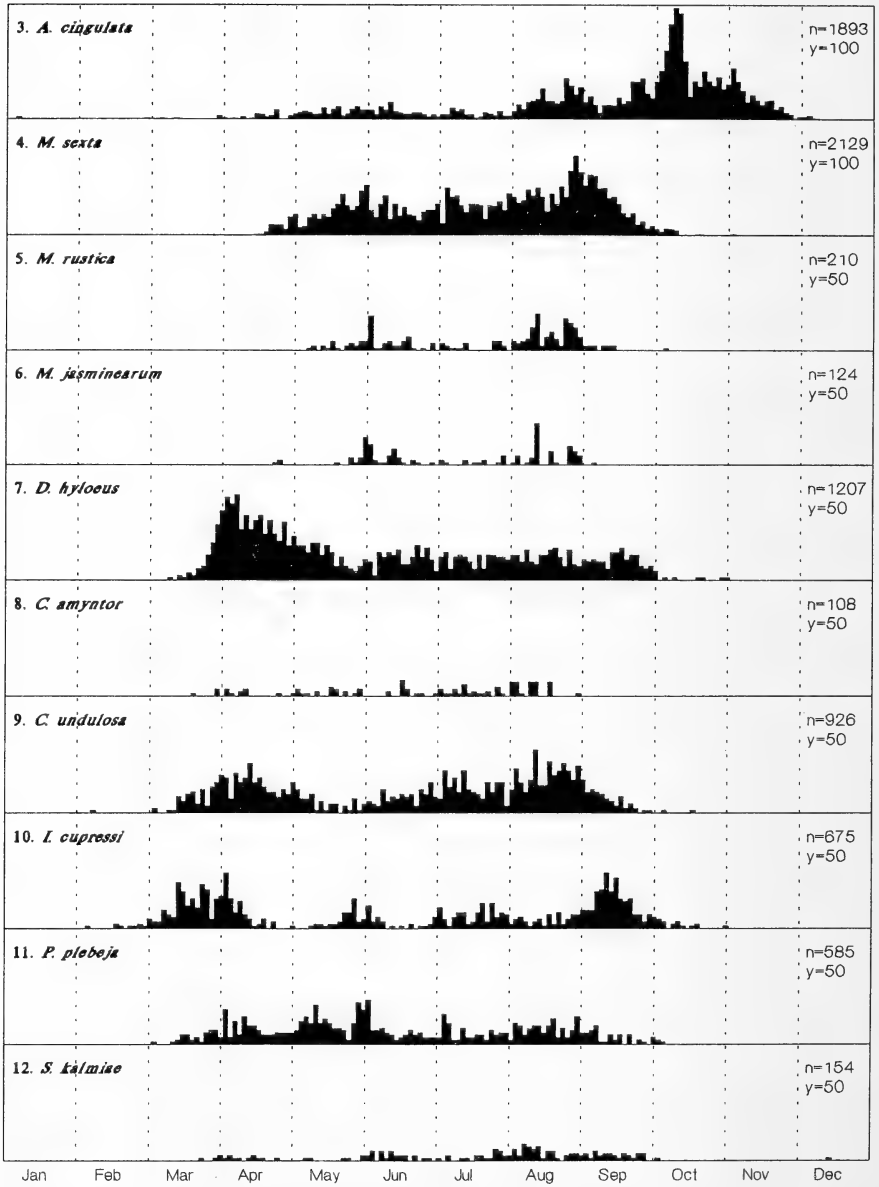
Certain annual broods in some species also tend to be consistently small or large, and these relative brood sizes tend to repeat from year to year. For example, the fourth annual brood of *Darapsa myron* is typically the smallest, and is bordered by the two largest broods (three and five) (Figs. 29, 33). For *Sphecodina abbottii*, the second and especially the fourth broods are reduced (the fourth may in fact represent a frequently observed partial brood). The composite-year graph for *S. abbot-tii* (Fig. 25) masks these small broods, but the trends are more apparent when individual years are examined (cf. Fig. 34). A similar pattern can be seen in *D. pholus*, in which broods occur at approximately monthly intervals. Broods one, three, five, and six are usually more populous than broods two, four, and seven. On the composite-year graph (Fig. 30), broods five through seven merge together and give the impression of a single, final brood (cf. Fig. 35). Why some multibrooded species have

TABLE 1. Numbers and identities of Sphingidae sampled from 1970 to 1995 in Louisiana, by month. B = new state records from the authors' sampling. Other letters represent species recorded for Louisiana in the literature but not sampled by the authors: V = von Reizenstein (1863, 1881), J = Jung (1950), O = Ottolengui (1894). Some specimens recorded as *Lapara confierarum* from 1970-1985 represent *L. phaeobrachycerous*, since records of the two were not segregated until 1986; records for *L. phaeobrachycerous* represent only those for the period 1986-1995. Asterisks indicate species sampled outside the period 1970-1995: *Eumorphia labruscae* is included on the basis of a single female taken in 1964 at Houma, Terrebonne Parish (month uncertain), and *Pachylia ficus* is included on the basis of a single male taken in 1996 at New Orleans.

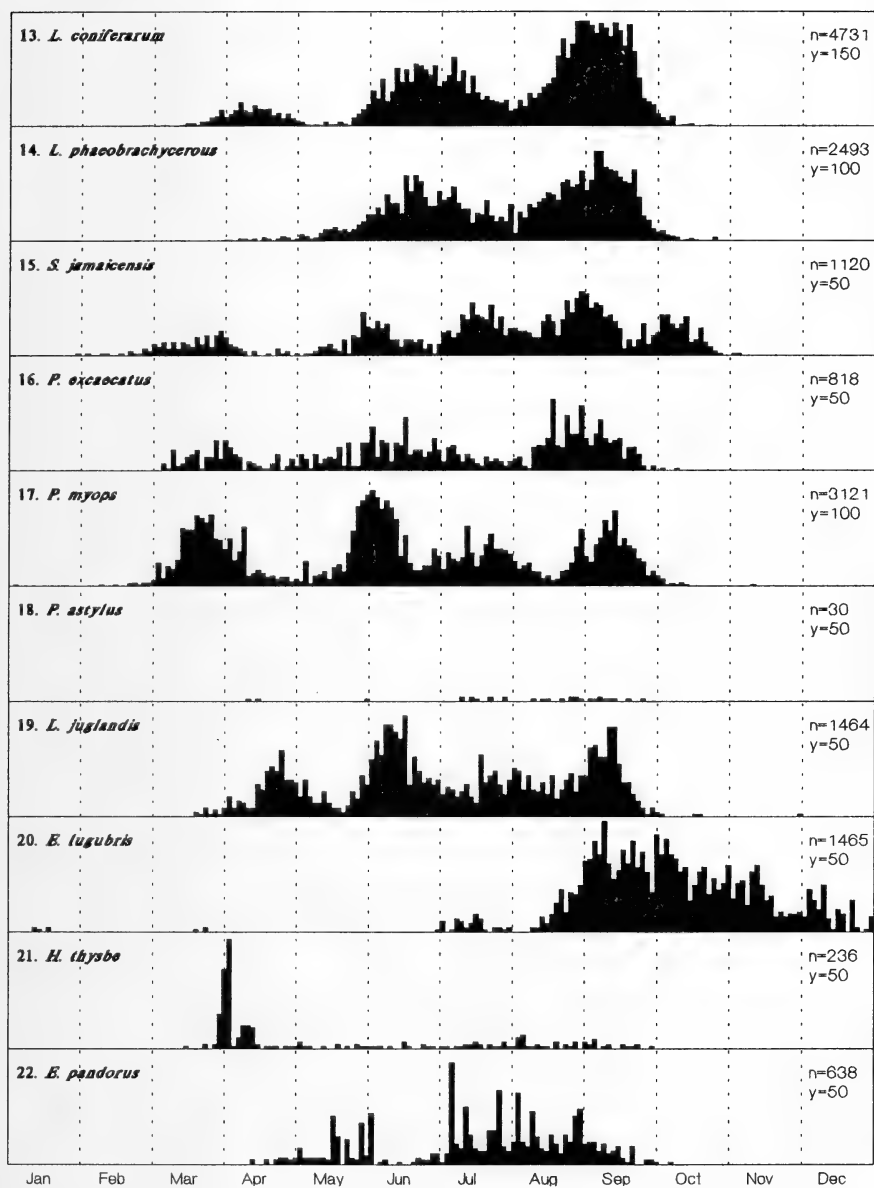
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1. <i>Agrius cingulata</i> (F.)	2	1	6	31	110	93	75	295	302	761	212	5	1893
2. <i>Manduca sexta</i> (L.)	0	0	0	64	342	320	413	600	370	19	1	0	2129
3. <i>M. quinquemaculata</i> (Haw.)	0	0	1	6	4	4	7	14	20	4	0	0	60
4. <i>M. rustica</i> (F.)	0	0	0	0	26	43	22	108	10	1	0	0	210
5. <i>M. jaminearum</i> (Guer.)	0	0	0	3	20	32	14	54	1	0	0	0	124
6. <i>Dolba hylaeus</i> (Drury)	0	0	80	388	165	144	145	151	128	6	0	0	1207
7. <i>Ceratomia amyntor</i> (Geyer)	0	0	4	10	21	15	27	31	0	0	0	0	108
8. <i>C. undulosa</i> (Wlk.)	0	1	83	185	64	104	162	258	67	2	0	0	926
9. <i>C. catalpae</i> (Bdv.) ^B	0	0	0	4	1	7	8	11	19	1	0	0	51
10. <i>C. hageni</i> (Grt.) ^B	0	0	0	2	3	4	2	1	0	0	0	0	12
11. <i>Isoparce cupressi</i> (Bdv.)	0	9	156	84	48	34	90	62	175	17	0	0	675
12. <i>Paratreita plebeja</i> (F.)	0	0	35	100	148	80	72	106	41	3	0	0	585
13. <i>Sphinx eremitus</i> (Hbn.) ^B	0	0	0	0	0	0	0	3	0	0	0	0	3
14. <i>S. leucophaeta</i> Clem. ^V	0	0	0	0	0	0	0	0	0	0	0	0	0
15. <i>S. chersis</i> (Hbn.) ^V	0	0	0	0	0	0	0	0	0	0	0	0	0
16. <i>S. francii</i> Neum.	0	0	0	0	3	4	1	4	0	0	0	0	12
17. <i>S. kalmiae</i> J. E. Smith	0	0	3	12	6	25	23	52	31	1	0	1	154
18. <i>S. drupiferarum</i> J. E. Smith ^V	0	0	0	0	0	0	0	0	0	0	0	0	0
19. <i>Lapara confierarum</i> (J. E. Smith)	0	2	105	500	241	1648	1286	2275	2402	59	0	0	8518
20. <i>L. phaeobrachycerous</i> Brou	0	0	1	43	205	661	520	860	902	37	0	0	3229
21. <i>Smerinthus jamaicensis</i> (Drury)	1	13	92	27	80	112	227	248	187	131	2	0	1120
22. <i>Paonias excrucatus</i> (J. E. Smith)	0	0	75	61	94	167	84	227	153	3	0	0	864
23. <i>P. myops</i> (J. E. Smith)	1	15	623	256	432	651	505	303	555	14	1	0	3356
24. <i>P. astylus</i> (Drury) ^B	0	0	0	2	1	0	9	9	9	0	0	0	30
25. <i>Loathoe juglandis</i> (J. E. Smith)	0	0	14	191	138	402	217	226	272	3	1	0	1464

TABLE 1. (continued)

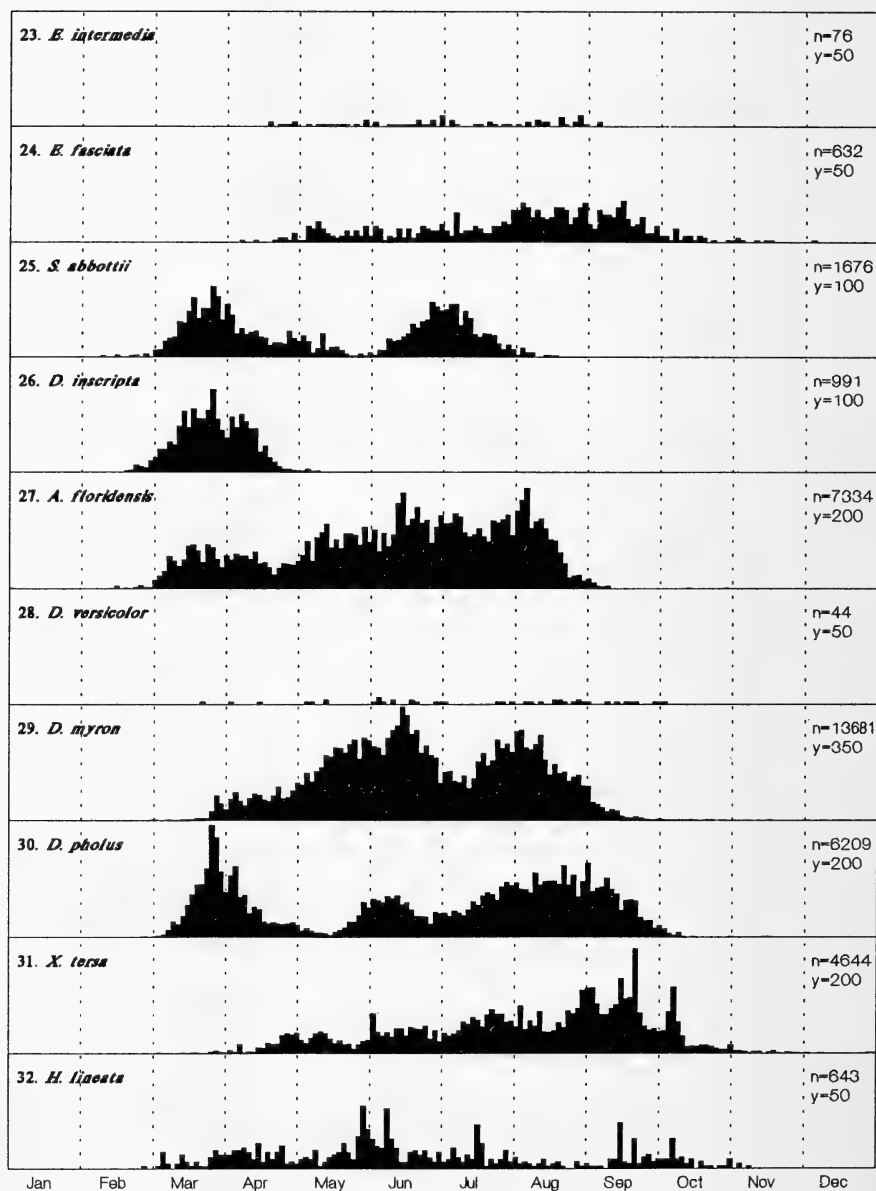
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
26. <i>Pachyspinx modesta</i> (Harr.)	0	0	1	0	2	5	3	18	0	0	0	0	29
27. <i>Pseudospinx tetrio</i> (L.)	0	0	0	0	0	0	0	0	0	0	2	0	2
28. <i>Erynnis alope</i> (Drury) ^l	0	0	0	0	0	0	0	0	0	0	0	0	0
29. <i>E. lassauxi</i> (Bdv.) ^l	0	0	0	0	0	0	0	0	0	0	0	0	0
30. <i>E. ello</i> (L.)	0	0	0	0	0	1	1	1	0	2	1	0	6
31. <i>E. obscura</i> (F.)	0	0	0	0	1	0	0	1	1	1	1	0	5
32. <i>E. domingonis</i> (Bd.) ^l	0	0	0	0	0	0	1	0	0	0	0	0	1
33. <i>Pachylia ficus</i> (L.) ^l	1	0	0	0	0	0	0	0	0	0	0	0	1
34. <i>Aellopos titan</i> (Cram.) ^v	0	0	0	0	0	0	0	0	0	0	0	0	0
35. <i>A. fadus</i> (Cram.) ^v	0	0	0	0	0	0	0	0	0	0	0	0	0
36. <i>Enyo lugubris</i> (L.)	5	0	3	0	0	1	45	152	505	411	223	120	1465
37. <i>Hemaris thysbe</i> (F.)	0	0	32	111	14	12	22	29	16	0	0	0	236
38. <i>H. diffinis</i> (Bdv.)	0	0	0	1	2	1	76	15	11	1	0	0	107
39. <i>Eumorphia satellita licaon</i> (Cram.) ^o	0	0	0	0	0	0	0	0	0	0	0	0	0
40. <i>E. pandorus</i> (Hbn.)	0	0	0	15	97	44	207	203	71	1	0	0	638
41. <i>E. intermedia</i> (B. P. Clark)	0	0	0	7	12	21	12	22	2	0	0	0	76
42. <i>E. achemon</i> (Drury)	0	0	0	0	1	0	0	2	0	0	0	0	3
43. <i>E. vittis</i> (L.)	0	0	0	0	0	0	0	0	5	0	0	0	5
44. <i>E. fasciatus</i> (Sulz.)	0	0	0	13	67	70	105	202	142	26	6	1	632
45. <i>E. labruscae</i> (L.) ^l	0	0	0	0	0	0	0	0	0	(1)	(1)	0	1
46. <i>Sphecodina abbottii</i> (Swainson) ^l	0	9	513	294	117	350	372	21	0	0	0	0	1676
47. <i>Deidamia inscripta</i> (Harr.)	0	28	606	350	7	0	0	0	0	0	0	0	991
48. <i>Amphion floridensis</i> B. P. Clark	1	27	902	823	1590	1906	2055	1332	28	2	0	0	8666
49. <i>Proserpinus gaurae</i> (J. E. Smith) ^v	0	0	0	0	0	0	0	0	0	0	0	0	0
50. <i>Darapsa versicolor</i> (Harr.)	0	0	1	2	4	12	4	13	7	1	0	0	44
51. <i>D. myron</i> (Cram.)	0	0	206	1436	4090	4937	4096	3709	333	13	1	0	18821
52. <i>D. pholus</i> (Cram.)	0	1	1043	728	312	775	967	1477	870	34	2	0	6209
53. <i>Xylophanes pluto</i> (F.)	0	0	0	0	0	1	0	0	0	0	0	0	1
54. <i>X. tersa</i> (L.)	0	0	12	222	359	599	867	1020	1297	440	29	3	4848
55. <i>Hyles lineata</i> (F.)	0	1	48	94	124	139	88	30	69	47	3	0	643
Total records	11	107	4645	6065	8951	13424	12830	14145	9001	2041	485	130	71836
Species per month	6	11	25	32	37	36	37	39	32	28	14	5	



FIGS. 3–12. Phenologies of Louisiana Sphingidae: composite-year graphs for individual species, data summed from 1970–1995. Specimens sampled (n) and number of specimens represented by entire vertical axis (y) given at right. 3, *Agrius cingulata*; 4, *Manduca sexta*; 5, *M. rustica*; 6, *M. jaminearum*; 7, *Dolba hyloeus*; 8, *Ceratomia amyntor*; 9, *C. undulosa*; 10, *Isoparce cupressi*; 11, *Paratrea plebeja*; 12, *Sphinx kalmiae*.



FIGS. 13–22. Phenologies of Louisiana Sphingidae: composite-year graphs for individual species, data summed from 1970–1995. Specimens sampled (n) and number of specimens represented by entire vertical axis (y) given at right. 13, *Lapara coniferarum*; 14, *L. phaeobrachycerous*; 15, *Smerinthus jamaicensis*; 16, *Paonias excaecatus*; 17, *P. myops*; 18, *P. astylus*; 19, *Laothoe juglandis*; 20, *Enyo lugubris*; 21, *Hemaris thysbe*; 22, *Eumorphia pandorus*.



FIGS. 23–32. Phenologies of Louisiana Sphingidae: composite-year graphs for individual species, data summed from 1970–1995. Specimens sampled (n) and number of specimens represented by entire vertical axis (y) given at right. 23, *Eumorphia intermedia*; 24, *E. fasciata*; 25, *Sphecodina abbottii*; 26, *Deidamia inscripta*; 27, *Amphion floridensis*; 28, *Darapsa versicolor*; 29, *D. myron*; 30, *D. pholus*; 31, *Xylophanes tersa*; 32, *Hyles lineata*.

reduced population sizes for certain broods remains unclear. No doubt climatic extremes (e.g., rainfall, drought) and biological influences (e.g., predators, parasites) play a role, but we neither systematically studied nor found obvious correlations between these factors and observed brood sizes and timings.

The approximate 30-day brood cycles that were exhibited by many species are not sampling artifacts related to the lunar cycle, as species attracted to fermenting bait showed the same cyclical patterns as those attracted to light. A good example is *E. lugubris* in 1991 (Fig. 36). This species is attracted to both light and bait. The initial 1991 brood occurred in early to mid July, roughly coinciding with a new moon. Broods two through five peaked at about 28-day intervals beginning in early September, and these subsequent brood peaks did not coincide with either new or full moons (persistent cold weather during December 1991 prevented collection of sixth brood specimens). Similarly, *L. phaeobrachycerous* Brou in 1991 (Fig. 37) showed brood peaks not correlated with lunar phase. Few specimens of the initial brood were collected in early May, as is normally true for this species, and the remaining four brood peaks occurred at about 30-day intervals between new and full moons, beginning in early June.

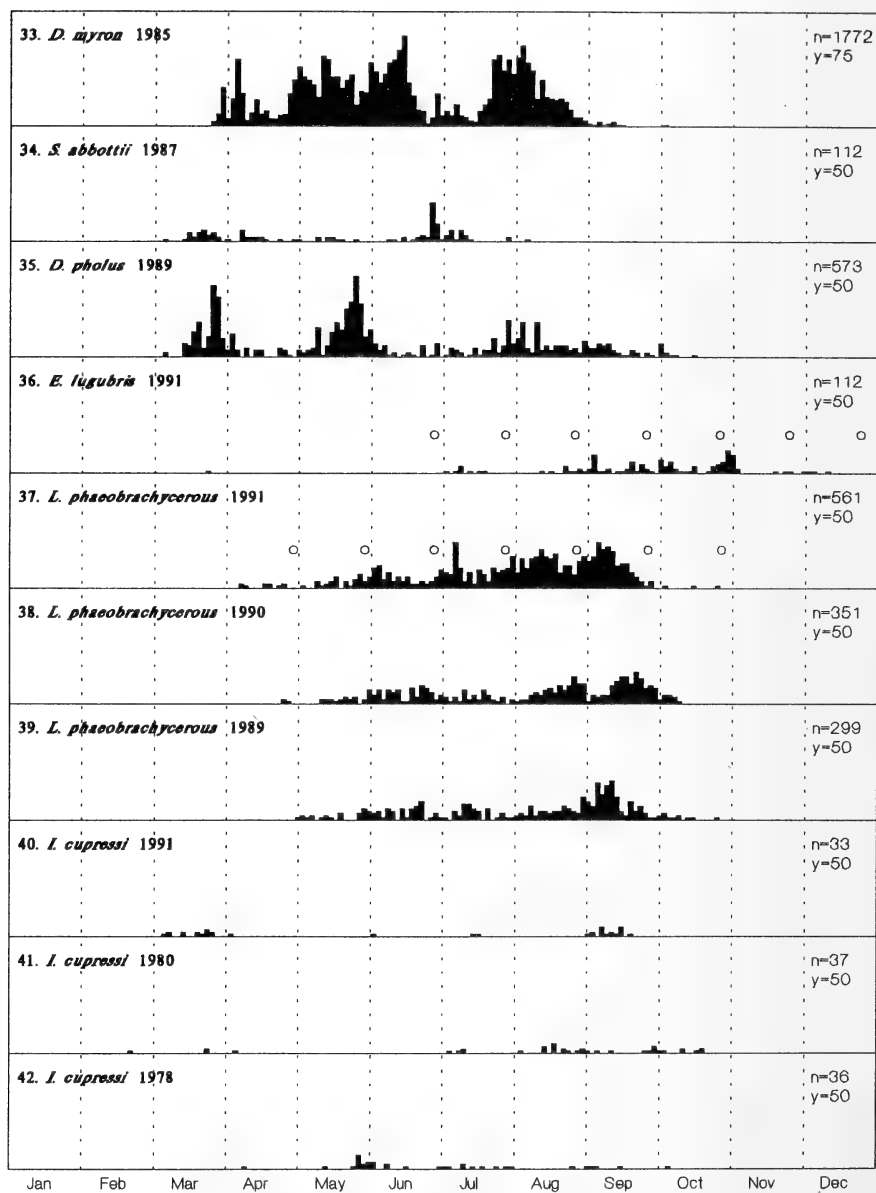
For species often seen only at low numbers, representative specimens for each brood were not observed in some years. An example is *Isoparce cupressi*. During 1991, only 14 specimens of the initial brood were taken (Fig. 40); a single specimen for the second brood; two specimens for the third brood; and 16 specimens for the fourth brood. In 1980 (Fig. 41), no specimens were collected at the usual emergence time of the second brood, though there were specimens representing broods three, four, and five. In 1978 (Fig. 42), the first and fifth broods were each represented by single specimens, whereas broods two, three, and four were represented by multiple specimens. In 1973 (Fig. 43), only broods two, three, and four were represented.

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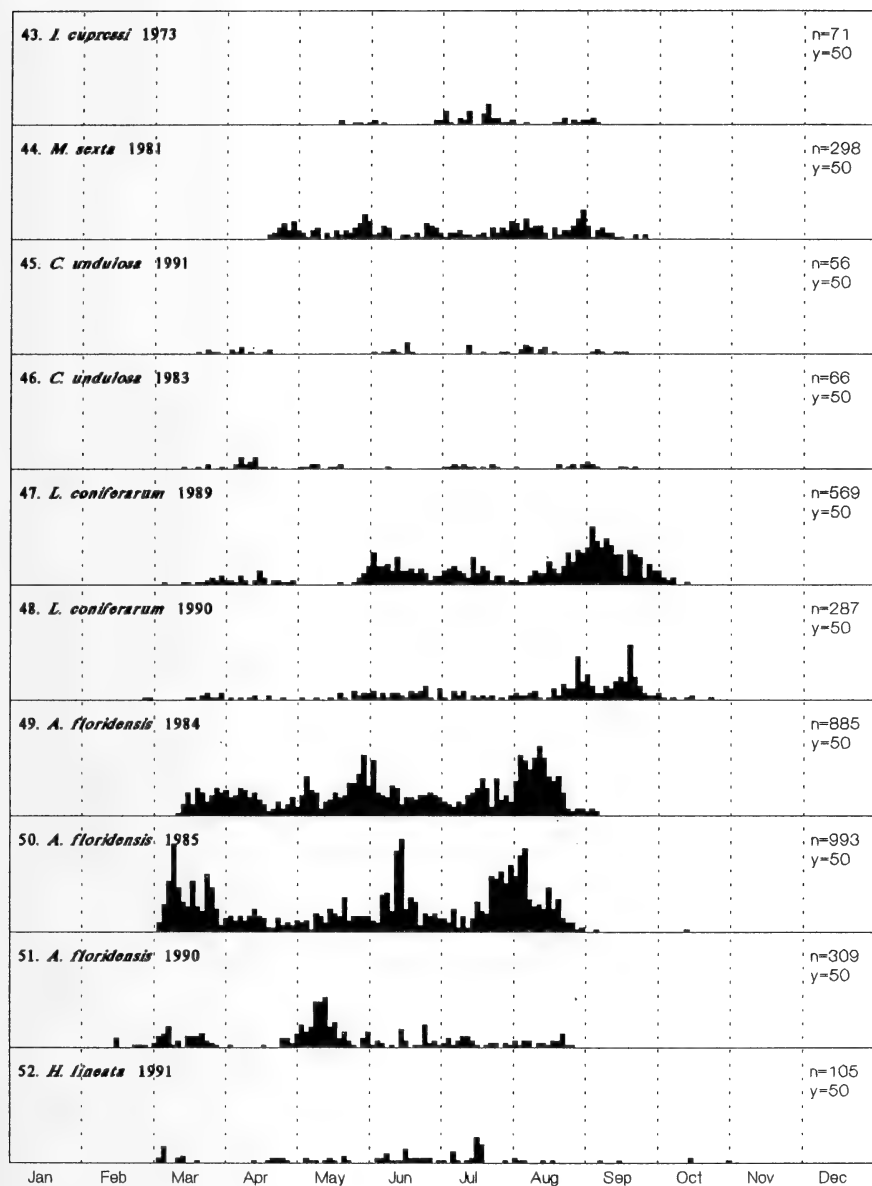
Agrius cingulata (F.) (Fig. 3): seven broods, first peaking late April to early May; peaks two through seven occur at approximately 30-day intervals, beginning early to mid-June; occasional December specimens may indicate partial emergence of an eighth brood.

Manduca sexta (L.) (Figs. 4, 44): five broods peaking at approximately 30-day intervals, beginning at the end of April; occasional October specimens may indicate partial emergence of a sixth brood; previously reported by Beutenmuller (1895) as double-brooded near New York City, and by Heitzman (1987) as having two or more broods in Missouri.

Manduca quinquemaculata (Haw.): five broods, first peaking approximately mid April; peaks two through five occur at approximately 30-day intervals, beginning early June; occasional October specimens may indicate partial emergence of a sixth brood; previously reported by Beutenmuller (1895) as double-brooded near New York City, and by Heitzman (1987) as having two or more broods in Missouri.



FIGS. 33–42. Phenologies of Louisiana Sphingidae: single-year graphs for individual species. Specimens sampled (n) and number of specimens represented by entire vertical axis (y) given at right. Full moons on Figs 36, 37 indicated by open circles (see text for elaboration). **33**, *Darapsa myron*, 1985; **34**, *Sphecodina abbottii*, 1987; **35**, *Darapsa pholus*, 1989; **36**, *Enyo lugubris*, 1991; **37**, *Lapara phaeobrachycerous*, 1991; **38**, *L. phaeobrachycerous*, 1990; **39**, *L. phaeobrachycerous*, 1989; **40**, *Isoparce cupressi*, 1991; **41**, *I. cupressi*, 1980; **42**, *I. cupressi*, 1978.



FIGS. 43-52. Phenologies of Louisiana Sphingidae: single-year graphs for individual species. Specimens sampled (n) and number of specimens represented by entire vertical axis (y) given at right. **43**, *Isoparce cupressi*, 1973; **44**, *Manduca sexta*, 1981; **45**, *Ceratomia undulosa*, 1991; **46**, *C. undulosa*, 1983; **47**, *Lapara confiferarum*, 1989; **48**, *L. confiferarum*, 1990; **49**, *Amphion floridensis*, 1984; **50**, *A. floridensis*, 1985; **51**, *A. floridensis*, 1990; **52**, *Hyles lineata*, 1991.

Manduca rustica (F.) (Fig. 5): four broods, first peaking at the end of May; peaks two through four occur at approximately 30-day intervals, beginning early July.

Manduca jasmineearum (Guer.) (Fig. 6): two broods, peaking early June and mid August; similar brood times occur for *S. frankii*; previously reported by Beutenmuller (1895) as probably double-brooded near New York City.

Dolba hyloeus (Drury) (Fig. 7): six broods, first peaking in early April; peaks two through six occur at approximately 30-day intervals, beginning mid-May; occasional October specimens may indicate partial emergence of a seventh brood; previously reported by Rowley (1899) as probably double-brooded in Missouri.

Ceratomia amyntor (Geyer) (Fig. 8): five broods, first peaking in early April; peaks two through five occur at approximately 30-day intervals, beginning mid-May; previously reported by Hodges (1971) as having two broods in the south, by Covell (1984) as having two broods, and by Heitzman (1987) as having two broods in Missouri.

Ceratomia undulosa (Wlk.) (Figs. 9, 45, 46): six broods, first peaking in early April; peaks two through six occur at approximately 30-day intervals; initial brood emergence varying by two weeks from year to year; previously reported by Beutenmuller (1895) as double-brooded near New York City, and by Hodges (1971) and Covell (1984) as having two broods.

Ceratomia catalpae (Bdv.): five broods, first peaking in mid April; peaks two through five occur at approximately 35-day intervals, beginning late May; previously reported by Hodges (1971) and Covell (1984) as having two broods.

Ceratomia hageni Grt.: four or more broods; additional records are needed; previously reported by Hodges (1971) and Covell (1984) as having two broods, and by Heitzman (1987) as having three broods in Missouri.

Isoparce cupressi (Bdv.) (Figs. 10, 40–43): usually four broods, protracted initial brood usually peaking third week of March; peaks two through four occur at approximately 50-day intervals, beginning late May; initial emergence peak varying by three weeks from year to year; affecting emergence time of subsequent broods (and probably why in some years there are specimens representing five broods); previously reported by Covell (1984) as having two broods.

Paratreia plebeja (F.) (Fig. 11): six broods, first peaking early to mid April; peaks two through six occur at approximately 30-day intervals, beginning five weeks later; previously reported by Beutenmuller (1895) as double-brooded near New York City, by Hodges (1971) as having two broods in the south, and by Holland (1903), Rothschild & Jordan (1903), and Covell (1984) as having two broods.

Sphinx frankii Neum.: two broods, peaking approximately mid June and mid August; previously reported by Hodges (1971) and Covell (1984) as having one brood and a partial second.

Sphinx kalmiae J. E. Smith (Fig. 12): six broods, first peaking early to mid April; remaining peaks at approximately 30-day intervals; previously reported by Beutenmuller (1895) as double-brooded near New York City, and by Hodges (1971) as probably having two broods.

Lapara confifarum (J. E. Smith) (Figs. 13, 47, 48): five broods, first peaking early to mid April (see Brou 1994); peaks two through five occur at approximately 30-day intervals, beginning mid-June; previously reported by Koebele (1881) as having at least two broods in the southern United States, and by Riotte (1972) as having two distinct flight periods in the south coastal states.

Lapara phaeobrachycerous Brou (Figs. 14, 37–39): five broods, first peaking about mid May (see Brou 1994); remaining peaks occur at approximately 30-day intervals.

Smerinthus jamaicensis (Drury) (Fig. 15): five or more broods, protracted initial brood peak approximately mid March; peaks two through four occur at approximately 45-day intervals, beginning early-June; November specimens may indicate a partial sixth brood; previously reported by Beutenmuller (1895) as being double-brooded near New York City, and by Heitzman (1987) as being multibrooded in Missouri.

Paonias excaecatus (J. E. Smith) (Fig. 16): four broods, first peaking late March; peaks two through four occur at approximately 45-day intervals, beginning early June; previously reported by Beutenmuller (1895) as double-brooded near New York City, by Rowley (1898)

as double-brooded in Missouri, by Hodges (1971) as having two broods in Florida, by Covell (1984) as having three broods, and by Heitzman (1987) as having several broods in Missouri.

Paonias myops (J. E. Smith) (Fig. 17): four broods, first peaking late March; peaks two through four occur at approximately 50-day intervals, beginning early June; previously reported by Beutenmuller (1895) as probably double-brooded near New York City, by Hodges (1971) as seemingly single-brooded, and by Heitzman (1987) as having multiple broods in Missouri.

Paonias astylus (Drury) (Fig. 18): four broods; limited data indicate it may have broods similar to other members of the genus; previously reported by Hodges (1971) as having two broods in Florida, and by Covell (1984) as having two broods.

Laothoe juglandis (J. E. Smith) (Fig. 19): four broods, peaking at approximately 45-day intervals, beginning late April; previously reported by Beutenmuller (1895) as double-brooded near New York City, by Hodges (1971) as having two broods in the south, by Covell (1984) as having three broods, and by Heitzman (1987) as having several broods in Missouri.

Pachysphinx modesta (Harr.): five broods, first peaking late March; peaks two through five occur at approximately 30-day intervals, beginning mid-May; previously reported by Beutenmuller (1895) as probably double-brooded near New York City, by Hodges (1971) as having two broods in Arkansas, Kansas, and perhaps Missouri, by Covell (1984) as having three broods, and by Heitzman (1987) as being multibrooded in Missouri.

Enyo lugubris (L.) (Figs. 20, 36): usually six broods, first peaking about mid July; peaks two through six occur at approximately 30-day intervals, beginning early September; broods five, six, and occasionally seven affected by cold weather during some years; previously reported by Holland (1903) as having two broods in Florida.

Hemaris thysbe (F.) (Fig. 21): six broods, first peaking end of March, and at approximately 30-day intervals; previously reported by Beutenmuller (1895) as double-brooded near New York City, by Rowley (1899) as double-brooded in Missouri, by Hodges (1971) as having two broods in the south, by Covell (1984) as having two broods, and by Heitzman (1987) as having three broods in Missouri.

Hemaris diffinis (Bdv.): four broods, first peaking mid April, and at approximately 50-day intervals; previously reported by Rowley (1899) as double-brooded in Missouri, by Hodges (1971) as double-brooded in the northern United States, and by Covell (1984) as having two broods.

Eumorpha pandorus (Hbn.) (Fig. 22): four broods, first peaking about mid May; peaks two through four occur at 30-day intervals, beginning early July; previously reported by Beutenmuller (1895) as double-brooded near New York City, and by Rowley (1899) as double brooded in Missouri.

Eumorpha intermedia (B. P. Clark) (Fig. 23): four broods, first peaking about mid May; peaks two through four occur at approximately 30-day intervals beginning late June.

Eumorpha fasciatus (Sulz.) (Fig. 24): six or more broods, first peaking in early May, and at approximately 30-day intervals; initial brood emergence varying by two weeks in any given year; November and December specimens may indicate partial emergence of seventh and eighth broods; previously reported by Hodges (1971) as having two broods in South Carolina, and Covell (1984) as having two broods.

Sphecodina abbottii (Swainson) (Figs. 25, 34): three or four broods, first peaking end of March, and at approximately 45-day intervals; initial brood emergence varying by more than two weeks in any given year; broods two and four occur at low numbers; previously reported by Heitzman (1987) as having two broods in Missouri.

Deidamia inscripta (Harr.) (Fig. 26): one brood, peaking at the end of March; previously reported by Beutenmuller (1895) as probably double-brooded near New York City, and by Hodges (1971) as having one brood.

Amphion floridensis B. P. Clark (Figs. 27, 49–51): six broods, first peaking end of March, and at approximately 25-day intervals; initial brood emergence varying by two weeks in any given year; previously reported by Hodges (1971) as multiple-brooded in the south, and by Covell (1984) as having two broods.

Darapsa versicolor (Cram.) (Fig. 28): five or more broods, peaking at approximately 30-day intervals; additional records are needed; previously reported by Beutenmuller (1895) as double-brooded near New York City, and by Forbes (1948) as having two broods.

Darapsa myron (Cram.) (Figs. 29, 33): five or more broods, first peaking early to mid April, and at approximately 30-day intervals; initial brood emergence varying by more than two weeks in any given year; September and October specimens may represent partial emergence of sixth and seventh broods; previously reported by Beutenmuller (1895) as double-brooded near New York City, by Hodges (1971) as double-brooded in New York and South Carolina, and by Covell (1984) as having two broods.

Darapsa pholus (Cram.) (Figs. 30, 35): seven broods, first peaking end of March, and at approximately 30-day intervals; initial brood emergence varying by two weeks in any given year; second, fourth, and seventh broods usually at low numbers; November specimens may represent partial emergence of an eighth brood; previously reported by Beutenmuller (1895) as double-brooded near New York City, by Rowley (1898) as having two broods in Missouri, and by Lutz (1948), Hodges (1971), and Covell (1984) as having two broods.

Xylophones tersa (L.) (Fig. 31): six or more broods, first peak variable, usually at the start of May; peaks two through six occur at approximately 30-day intervals, beginning mid-June; occasional late year specimens appear, probably representing partially emergent subsequent brood(s).

Hyles lineata (F.) (Figs. 32, 52): eight or nine broods, variable first peak late February to early March, and at approximately 30-day intervals; previously reported by Beutenmuller (1895) as double-brooded near New York City.

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GENERAL NOTES

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CALLOPHRYS ERYPHON (LYCAENIDAE) COLONIZES URBAN AND SUBURBAN SAN FRANCISCO BAY AREA, CALIFORNIA, USING PLANTED MONTEREY PINE

Additional key words: *Incisalia*, biogeography, dispersal.

The western banded elfin, *Callophrys (Incisalia) eryphon* (Boisduval), is widespread in western North America, mainly in Transition Life Zone and montane regions, where its larvae feed on various conifers, primarily Pinaceae (Hardy 1959, McGugan 1958, Newcomer 1973). In California, this butterfly occurs from the Cascade Range southward along both sides of the Sierra Nevada and in the North Coast Ranges, mostly at elevations of 1000–2500 m, to the San Bernardino and San Jacinto Mountains of southern California above 2000 m (Essig Museum specimens). Along the north coast, natural populations of *C. eryphon* range nearly to sea level, near Plantation, Sonoma Co. and Inverness, Marin Co., in association with Bishop pine, *Pinus muricata*. The elfin may have been native on the Peninsula south of San Francisco because there are three specimens in the Museum of Comparative Zoology, Harvard University, labelled "San Mateo, Cal. A. Agassiz," probably dating from the 19th century. However, there are no modern records from the Peninsula or Santa Cruz Mountains area (Steiner 1990). In Monterey County, a population occurs at the S. F. B. Morse Botanical Reserve on the Monterey Peninsula in association with an isolated colony of native Bishop pine (J. Lane pers. comm., LACM specimens), but *C. eryphon* is not known from Monterey pine (*Pinus radiata*) there or at the other native stands, nor from other native pines of central coastal California.

There are old records (1929 to 1950) from San Francisco (Steiner 1990); included are specimens collected at The Presidio, where Monterey pine has been grown for more than a century. However, H. Reinhard (unpubl. data), J. E. Hafernik (in litt.), and I have failed to find *C. eryphon* there in recent years. According to H. H. Behr, conifers grew on Lone Mountain at the western edge of the city in the late 1800's (Howell et al. 1958). These likely were *Pinus muricata* or *P. radiata*, Howell et al. reasoned, so it is possible that a colony of *C. eryphon* existed there, and its descendants adopted plantings of Monterey pine at The Presidio. However, because there are no specimens taken by H. E. Cottle, F. X. Williams, or other early 20th century collectors in San Francisco (Steiner 1990), it seems likely that the later records represent an adventive colony originating from native conifers of Marin County 15–30 km to the northwest, the direction of prevailing winds.

In recent years the western banded elfin has expanded its range in the San Francisco Bay region. It evidently occurred naturally inland in Marin County in association with Bishop Pine or Douglas-fir (*Pseudotsuga menziesii*), because the butterfly was collected at Mill Valley on the east side of Mt. Tamalpais in 1908. In recent decades, *C. eryphon* has been discovered successively southeastward from Mt. Tamalpais, in suburban areas distant from native conifers: on the eastern bay shore of Marin County at Strawberry Point in the grounds of a seminary in 1973 and in an urban yard in Belvedere in 1980; and across the bay, at Pt. Molate, Contra Costa Co. in 1989, in association with young Monterey pine in a park that was developed in the 1960's. In 1994 and 1995 *C. eryphon* appeared at several sites on both sides of the Berkeley Hills (Fig. 1). There is no record of this butterfly in the East Bay area (Contra Costa and Alameda counties) prior to 1989 (Opler & Langston 1968, Steiner 1990).

During 1994, single females were observed in urban gardens in Kensington and Berkeley, and east of the Berkeley Hills at San Pablo Reservoir males perched on understory shrubs in a mature Monterey Pine woods planted more than 50 years ago. Additional individuals were encountered on four dates in 1995: near Pt. Richmond, on the University of California (UC) campus, in Strawberry Canyon at the UC Botanic Garden, and at 425 m elevation in the Berkeley Hills near the southern end of Grizzly Peak Blvd. At each of these East Bay sites, adults were active in the vicinity of *Pinus radiata*.

Any of these populations could have much older origins than the records document.



FIG. 1. Central California, showing positions of counties mentioned in the text. Inset (below) depicts spatial and temporal distribution of *Callophrys eryphon* in Marin, San Francisco, Contra Costa, and Alameda counties adjacent to San Francisco Bay. Presumed native colonies in Marin County (filled symbols) are associated with native conifers; dated localities (half-filled symbols) refer to adventive colonies associated with Monterey pine plantings; no *C. eryphon* were seen at several peripheral East Bay sites in March–April 1995 (open symbols).

Nevertheless, because there is a long history of extensive Monterey pine planting in the cities around San Francisco Bay, in gardens, parks, at reservoirs, etc., the lack of older records suggests that the recent collections of *C. eryphon* reflect recent range extension. In 1994–95, the butterfly was encountered in the Berkeley area by four observers independently, one a novice collector in an introductory entomology course, each unaware of any prior occurrence of *C. eryphon* in the area. The evidence indicates the elfin has become established in Contra Costa and Alameda counties in quite recent years.

If this is true, why did the butterfly fail to colonize *Pinus radiata*, other than in San Francisco, at a much earlier date? Although *Callophrys eryphon*, *Pinus radiata*, and *P. ponderosa* are native species in central California, none occurred naturally in the East Bay area. Thus, this adaptation to non-native situations may be comparable to that of many in-

roduced insects, which undergo a sequence of introduction-establishment, then a long period of naturalization, followed by rapid range extension. Such delayed ecogeographical expansions are believed to involve increased genetic fitness to environmental conditions to which the founder populations were not adapted (e.g., Powell 1983, 1992). Presuming the eastward colonization of *C. eryphon* is recent, it seems reasonable to suppose that this handsome butterfly is becoming a widespread urban resident of the East Bay.

In the Canadian Forest Insect Survey, host tree preferences of *C. eryphon* in Alberta and British Columbia, based on 187 larval collections, were 83% on several species of pines (70% on lodgepole pine), 3% on other Pinaceae, namely Douglas-fir and western hemlock (*Tsuga heterophylla*), and 14% on *Thuja plicata* (Cupressaceae) (McGugan 1958). In California, there are no records of larval *C. eryphon* collections from Pinaceae other than *Pinus* (Garth & Tilden 1986, Powell & De Benedictis 1995).

Collection data for San Francisco Bay region (sr = sight record; sw = slightly worn; w = worn): Napa Co.: 2 mi. N Angwin, IV-26-73, IV-17-77, assoc. *Pinus ponderosa* (R. L. Langston). Sonoma Co.: 3 mi. W Plantation, V-5-55 (Langston); 4 mi. W Plantation, V-25-57 (J. Powell); Plantation, 800 ft. elev. V-16-58 (O. E. Sette), V-29-60 [P. A. Opler]. Marin Co.: Inverness, V-18-63 (C. A. Toschi), Inverness Ridge 800–1040', V-15-70, V-10-74, assoc. *Pinus muricata* (Powell), IV-25-76 (E. Schlinger, M. Helena), IV-22-78 (Powell), IV-26-96, in 1995 fire zone (Powell); Mt. Vision, IV-24-82 (Powell); 1 mi. SW Lagunitas, III-21-70 (Opler); Mill Valley, IV-4-1908 (F. X. Williams); Strawberry, Golden Gate Baptist Seminary, III-28/31-73 (♂♂ ♀♀) (V. & L. Donahue); Belvedere, IV-6-80 (sw ♂) (Powell). Contra Costa Co.: Pt. Molate Beach, IV-6-89 (sw ♂) (Powell); Pt. Richmond III-16-95 (sw ♀) (Powell); Kensington, IV-13-94 (sr) (Langston); San Pablo Reservoir, IV-18-94 (sw ♂♂) (Powell); Berkeley Hills, nr. jct. Grizzly Peak-Skyline Blvds., IV-14-95 (sw ♀) (Powell). Alameda Co.: Berkeley, nr. La Loma Park, IV-30-94 (w ♀) (D. Rubinoff); UC Botanic Garden, Strawberry Cyn., III-28-95 (sr), IV-10-95 (sw ♀), III-6-96 (sr) (Powell); UC Campus, IV-5-95 (w ♀) (K. Wong). San Francisco Co.: San Francisco, III-29-1929 (W. D. Field), III-15-1931 (R. G. Wind), V-5-35 (M. Doudoroff); Presidio, IV-16-49 (L. I. Hewes), IV-12-50 (E. S. Ross), Presidio nr. Baker Beach, IV-15-50 (J. W. Tilden).

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DIURNAL LEPIDOPTERA OF NATIVE AND RECONSTRUCTED PRAIRIES IN EASTERN MINNESOTA

Additional key words: surveys, species richness, vagility.

Prairie butterflies are subjects of increasing conservation concern. Their habitat has been greatly diminished, and their ability to survive on managed sites and to colonize new sites or recolonize old ones is in doubt (Opler 1991). In this paper I report on and compare the diurnal Lepidoptera communities of both native and reconstructed prairies in Minnesota.

I collected insects from the flowers of 58 forb species in four native prairie sites and four prairie reconstructions (former agricultural areas recently replanted to prairie) during the summers of 1990, 1991 and 1992. The sites are described in Table 1. Insects were collected between 0900 h and 1600 h on sunny or partly cloudy days when the temperature was between 20° and 35° C. Collections were made from late May to late September. I made one 15 min aerial net collection of insects on the flowers of each forb species with at least 100 flowers or inflorescences open, for a total of 507 collections from all forb species in all sites over the three summers. Thus, the number of collections made from a site was closely related to the number of forb species present in populations large enough to produce 100 or more flowers. Although only a small fraction of the Lepidoptera present on a site can be sampled by daylight collections, many of the species of conservation concern are diurnal.

The 507 collections yielded 3702 insects representing 305 species; 295 of these were identified at least to genus (Reed 1995). There were 118 Lepidoptera individuals representing 28 species: 24 butterflies and four diurnal moths (Table 2). Insect vouchers are deposited in the University of Minnesota Insect Museum, and plant vouchers are in the University of Minnesota Herbarium.

Collections in native sites produced greater species richness than in reconstructed sites: 73 individuals and 21 species in 218 15-min collections from native sites, compared to 45 individuals and 16 species in 289 collections from reconstructions. Five of the 28 species collected were described as prairie obligates by Orwig (1992): *Callophrys gryneus* (Hubner), *Hesperia l. leonardus* Harris, *H. l. pawnee* Dodge, *Polites origines* (Fabr.) and *Satyrus edwardsii* (Grote & Robinson) and an additional four species were described as remnant-restricted by Panzer et al. (1995): *Euphyes conspicua* (Edw.) *Harkenclenus titus* (Fabr.), *Speyeria aphrodite* (Fabr.) and *Thorybes pylades* (Scudder). Of these nine species, eight were collected from native sites only, none from reconstructions only, and one was collected from both native and reconstructed sites. Of the 19 species not considered site-restricted, four were collected from native sites only, seven from reconstructions only, and eight from both native and reconstructed sites (Table 3).

Management practices do not appear to account for the differences in species presence among sites. There are no obvious differences in management between native sites and reconstructions as a group: the large sites are burned in sections, while the small sites

TABLE 1. Descriptions of Minnesota prairie sites at which Lepidoptera collections were made. Area column gives sizes of entire site/specific area where collections were made. Plant abbreviations: 1, *Achillea millefolium*; 2, *Agastache foeniculum*; 3, *Allium canadense*; 4, *Amorpha canescens*; 5, *Anemone canadensis*; 6, *Aquilegia canadensis*; 7, *Aster ericoides*; 8, *Aster ontariensis*; 9, *Aster oolentangiensis*; 10, *Aster sericeus*; 11, *Aster simplex*; 12, *Berteroa incana*; 13, *Campanula rotundifolia*; 14, *Chrysopsis villosa*; 15, *Cirsium arvense*; 16, *Cirsium discolor*; 17, *Coreopsis palmata*; 18, *Crepis tectorum*; 19, *Dalea purpurea*; 20, *Dalea villosa*; 21, *Desmodium canadense*; 22, *Erigeron strigosus*; 23, *Galium boreale*; 24, *Grindelia squarrosa*; 25, *Helianthus rigidus*; 26, *Helianthus tuberosus*; 27, *Helopsis helianthoides*; 28, *Liatris aspera*; 29, *Liatris punctata*; 30, *Liatris pycnostachya*; 31, *Lithospermum canescens*; 32, *Lupinus perennis*; 33, *Melilotus alba*; 34, *Melilotus officinalis*; 35, *Mirabilis nyctaginea*; 36, *Monarda fistulosa*; 37, *Nepeta cataria*; 38, *Penstemon grandiflorus*; 39, *Phlox pilosa*; 40, *Potentilla arguta*; 41, *Potentilla recta*; 42, *Pycnanthemum virginianum*; 43, *Ratibida pinnata*; 44, *Rosa blanda*; 45, *Rubus occidentalis*; 46, *Rudbeckia hirta*; 47, *Solidago canadensis*; 48, *Solidago nemoralis*; 49, *Solidago rigida*; 50, *Solidago speciosa*; 51, *Stachys palustris*; 52, *Sysirinchium campestre*; 53, *Trifolium pratense*; 54, *Verbena hastata*; 55, *Verbena stricta*; 56, *Vernonia fasciculata*; 57, *Vicia americana*; 58, *Zizia aurea*.

Site	County: location	Prairie type	Area, hectares	Date Planted	Management, last burn	Surroundings	Forbs on site	No. of visits/collections
Reconstructions								
Afton State Park (ASP)	Washington: NE 1/4 Sect. 10, T27N R20W	mesic	4.8/4.8	1981	mowing, then burning 1989	old fields, woods, oak savanna remnant	19, 36, 43, 46, 54	12/17
Carpenter Nature Center (CARP)	Washington: NE 1/4 Sect. 8, T27N R20W	mesic	32.4/16.2	1988-1991	mowing, then burning of sections, then	corn and soybeans	1, 2, 7, 11, 15, 16, 19, 22, 25, 26, 27, 30, 34, 36, 40, 41, 43, 44, 46, 47, 49, 50, 51, 53, 55, 58	27/89
Crow Hassan Park Reserve (CHR)	Hennepin: NW 1/4 Sect. 19, T120N R23W	sand-mesic	243/10	1976-present	burning by sections 1991	Restored deciduous woods	1, 2, 3, 4, 5, 7, 9, 10, 14, 17, 19, 25, 26, 27, 28, 30, 32, 33, 34, 35, 36, 38, 39, 40, 43, 44, 46, 47, 49, 50, 52	23/107

TABLE 1. (continued)

Site	County: location	Prairie type	Area, hectares	Date Planted	Management, last burn	Surroundings	Forbs on site	No. of visits/ collections
Long Lake Regional Park (LLRP)	Ramsey: SE 1/4 Sect. 17, T30N R23W	xeric- mesic	2.8/2.8	1987	burning; 1992	Oak savanna remnant; wetland, lawns	1, 2, 3, 4, 7, 9, 10, 11, 12, 14, 18, 19, 20, 21, 22, 24, 25, 27, 33, 34, 36, 38, 42, 46, 47, 48, 49, 50, 58	12/76
Native prairie sites								
Afton Remnant (AREM)	Washington: N 1/2 Sect. 35, T28N R20W	bluff/ mesic	1.6/1.6	—	brush cutting and burning since 1987; 1989	St. Croix bluff; deciduous woods	1, 2, 4, 9, 16, 36, 37, 42, 46, 47, 48, 50, 54	12/49
Cedar Creek Natural History Area (CC)	Anoka: S 1/2 Sect. 34, T34N R 23W	sand	60.7/5	—	burning by sections, 1990	oak savanna	4, 9, 19, 25, 28, 31, 36, 38, 39, 42, 46, 47, 48, 49, 51,	21/62
Point Douglas Cemetery (CEM)	Washington: SE 1/4 Sect. 5, T27N R20W	mesic	0.4/0.4	—	brush cutting and burning since 1988; 1989	corn, soybeans, part of CARP planted in 1991	7, 9, 11, 21, 23, 25, 26, 27, 36, 43, 44, 47, 49, 50, 57	21/50
Lost Valley State Natural Area (LV)	Washington: S 1/2 Sect. 21 and N 1/2 Sect. 22, T27N R20W	bluff	40.5/7	—	brush cutting burning by sections since 1991; 1992	Old field, woods, hay field	1, 4, 6, 7, 8, 9, 10, 13, 16, 25, 28, 29, 36, 37, 42, 43, 45, 47, 49, 50, 56, 58	21/57

TABLE 2. Scientific and common names of Lepidoptera collected in this study. Nomenclature follows Scott (1984), Opler & Krizek (1984) and Covell (1984).

Hesperiidae

Atrytone logan (Edw.), Delaware Skipper
Euphyes conspicua (Edw.), Black Dash
Euphyes vestris (Boisd.), Dun Skipper
Hesperia leonardus leonardus Harris, Leonard's Skipper
Hesperia leonardus pawnee Dodge, Pawnee Skipper
Polites coras (Cr.), Peck's Skipper
Polites origines (Fabr.), Crossline Skipper
Polites themistocles (Latr.), Tawny-Edged Skipper
Wallengrenia egeremet (Scudder), Broken Dash
Epargyreus clarus (Cr.), Silver Spotted Skipper
Thorybes pylades (Scudder), Northern Cloudy Wing

Pieridae

Colias eurytheme Boisd., Orange Sulphur
Colias philodice Godart, Clouded Sulphur

Lycaenidae

Celastrina ladon (L.), Spring Azure
Satyrrium edwardsii (Gr. & Rob.), Edwards' Hairstreak
Callophrys gryneus (Hubner), Olive Hairstreak
Harkenclenus titus (Fabr.), Coral Hairstreak

Nymphalidae

Phyciodes tharos (Drury), Pearl Crescent
Nymphalis milberti (Godart), Milbert's Tortoiseshell
Vanessa cardui (L.), Painted Lady
Speyeria aphrodite (Fabr.), Aphrodite Fritillary
Speyeria cybele (Fabr.), Great Spangled Fritillary
Cercyonis pegala (Fabr.), Wood Nymph
Asterocampa celtis (Boisd. & Lec.), Hackberry Butterfly

Sphingidae

Hemaris diffinis (Boisd.), Snowberry Clearwing
Hemaris thysbe (Fabr.), Hummingbird Clearwing

Noctuidae

Alypia octomaculata Fabr., Eight-Spotted Forester

Ctenuchidae

Ciseps fulvicollis (Hubner), Yellow-Collared Scape Moth

(AREM, CEM, ASP and LLRP) are burned all at once. The ASP and CARP reconstructions were mowed for two years following planting, but now are managed by burning. Brush cutting is done as needed but does not replace burning on any site.

It is possible that the reconstructed sites do not provide suitable habitat for these obligate species. The reconstructions tend to be more mesic than the most species-rich native sites (CC and AREM), and five of the eight prairie obligates are reported to be restricted to xeric sites by Panzer et al. (1995): *Polites origines* and *Hesperia l. leonardus* to xeric prairie; *Harkenclenus titus* to xeric/mesic prairie; *Satyrrium edwardsii* to savanna; and *Thorybes pylades* to sand savanna. *Hesperia leonardus pawnee* and *Callophrys gryneus* also are found in xeric areas (Orwig 1992). Only two of the obligate species collected are reported by Panzer et al. from mesic sites: *Euphyes conspicua* from sedge meadow and

TABLE 3. Number of individual Lepidoptera species on each prairie site, and their nectar plants. Numeric plant abbreviations follow those given in Table 1. Superscript 1 = restricted to prairie habitats (Orwig 1992). Superscript 2 = high or moderate remnant reliance (Panzer et al. 1995).

Species	Native sites				Reconstructions				Nectar Plants
	AREM	CC	CEM	LV	ASP	CARP	CHR	LLRP	
<i>Alypia octomaculata</i>							1		34
<i>Atrytone logan</i>		4	1		2	3	2		15, 36, 39, 46, 55
<i>Asterocampa celtis</i>						1			36
<i>Callophrys gryneus</i>	2			1					42
<i>Celastrina ladon</i>	1								1
<i>Cercyonis pegala</i>							1	1	1
<i>Cisesepts fulvicollis</i>	2	1	6		1	4	2	1	1, 9, 28, 42, 46, 47, 48, 49, 50
<i>Colias eurytheme</i>		1		1	1	1	5		10, 11, 28, 29, 33, 46, 48
<i>Colias philodice</i>			1	5			1		9, 10, 25, 28
<i>Epargyreus clarus</i>	2				1				1, 36
<i>Euphyes conspicua</i> ²		1							39
<i>Euphyes vestris</i>	1	5			1				1, 36, 42, 46
<i>Harkenclenus titus</i> ²		4							28, 42
<i>Hemaris diffinis</i>	1		1			3			1, 36, 55
<i>Hemaris thysbe</i>	1	1							36
<i>Hesperia l. leonardus</i> ^{1,2}		2							28, 31
<i>Hesperia leonardus pawnee</i> ¹	2								16
<i>Nymphalis milberti</i>				1					8
<i>Phyciodes tharos</i>							1		1
<i>Polites coras</i>							1		38
<i>Polites origines</i> ^{1,2}	1								36
<i>Polites themistocles</i>		1							36
<i>Satyrrium edwardsii</i> ^{1,2}	4	11							1, 4, 42, 46
<i>Speyeria aphrodite</i> ²		2		1		1			28, 36
<i>Speyeria cybele</i>							1		36
<i>Thorybes pylades</i> ²	1	1							1, 39
<i>Vanessa cardui</i>			3			4	1	1	1, 14, 27, 28, 50, 53, 55
<i>Wallengrenia egeremet</i>					1	1	1		36

Speyeria aphrodite from mesic prairie (*S. aphrodite* was collected from the mesic reconstruction CARP—the only obligate individual found on a reconstruction). Beyond these associations with general prairie types, specific interactions with foodplants (both larval and adult), or larval-tending ants may be required for establishment of certain species, as has been demonstrated for other rare Lepidoptera species (Arnold 1983, Cushman & Murphy 1993). *Callophrys gryneus* may be absent from the reconstructions due to the absence of its larval foodplant, eastern red cedar (*Juniperus virginiana*) (Opler & Krizek 1984).

Alternatively, the obligate species may not have reached these reconstructions yet. Butterfly populations in some fragmented habitats have diminished mobility (Dempster 1991), and Cushman and Murphy (1993) suggest that dispersal ability is especially limited among lycaenids. Mobility may be influenced by species-specific behavior, such as reluctance to leave larval foodplants (Arnold 1983). Colonization of new habitat patches by these Lepidoptera may be an infrequent event that occurs during "rare years of explosive dispersal" as described by Ehrlich and Murphy (1987) for *Euphydryas editha*. More study of the basic biology and mobility of each species is required before we can predict whether prairie obligate butterflies will be able to colonize prairie reconstructions.

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YOU CAUGHT WHAT IN YOUR BACKYARD?

Additional key words: *Electrostrymon angelia*, *Ministrymon azia*, *Dryas iulia*, Florida, dispersal.

What butterflies are in your back yard? This question has been asked before in the pages of the *Journal* (Howe 1959) and many subsequent notes. Howe identified 64 butterfly species on a nine-acre plot in Kansas, at the time a truly impressive feat. We also



FIG. 1. *Electrostrymon angelia angelia*. Male, upper (left) and under (right) surfaces. Florida: Manatee Co.; 2 mi. E of Samoset, March 1992 (leg. J. Y. Miller).

been informally monitoring the butterfly faunas in two localities adjacent or close to our respective homes on the Florida Gulf Coast, one in Manatee County (Millers) and the other in Pinellas County (Anderson). These studies are recreational rather than scientific and undertaken more for curiosity than for any other reason.

The butterfly fauna of each area was reasonably well known as of early 1992, so it was surprising that each of us independently collected, during the latter half of that year, two species previously unrecorded from the west coastal area of the state. Both of these were lycaenids, and both have been recorded only recently from southeastern Florida and the Florida Keys.

Electrostrymon angelia angelia (Hewitson) has become a recent resident in southeastern Florida (Anderson 1974), and its known range extends along the Atlantic coast to about Fort Lauderdale. In March, and again in October 1992, Lee and Jackie Miller encountered this small hairstreak in their backyard nectaring on flowers of *Hyptis verticillata* Jacq. (Lamiaceae) (determination by R. Wunderlin, Univ. So. Florida). Anderson first found this species in Pinellas County in November 1992, nectaring on flowers of golden-rod, *Solidago* sp. (Asteraceae). Since the first sightings of this butterfly on the west coast of Florida were in March 1992, prior to the destruction wrought by Hurricane Andrew in southern Florida in August 1992, that storm could not have been the cause of this range extension. These specimens, one of which is illustrated here (Fig. 1), represent the first records of *E. angelia* for Pinellas and Manatee Counties, and resident populations, although quite small, have been seen in the area until present. The species was previously reported in Lee County on the Florida Gulf Coast by Heinrich in 1989 (see Baggett 1989).

Specimens of *Ministrymon azia* (Hewitson) were collected by Anderson during November 1992 in Pinellas County (Figs. 2, 3). About the same time in Manatee County, Lee and Jackie Miller made two positive sight records, with an additional sight record on the grounds of the Allyn Museum in Sarasota, Sarasota County. The first Manatee County specimen, a female, flew out of a tree and landed on the windshield of a car during a cool day; then it proceeded to thermoregulate there for several minutes with its wings alternately opening and closing, thus revealing the diagnostic ventral red spotband, and the gray-powdered upper hindwing that established its sex. These specimens, or their ancestors, might have been introduced through the actions of Hurricane Andrew, but due to their fresh condition, we suspect the species has been resident longer and simply avoided detection because of its small size and similar appearance to *Leptotes cassius theonius* (Lucas). There also is one record of *M. azia* from New Port Richey, Pasco County (Baggett 1989) captured late that year.

Both *E. angelia* and *M. azia* will feed as larvae on Brazilian pepper, *Schinus terebinthifolius* Raddi (Anacardiaceae), a ubiquitous weed in southern peninsular Florida that is well



FIGS. 2-3. *Ministrymon azia*. 2, male; 3, female (3). Upper (left) and under (right) surfaces. Both Florida: Pinellas Co.; St. Petersburg, November 1992 (leg. R. A. Anderson).

established on the Miller property, and *M. azia* also is known to feed upon *Leucaena leucocephala* (Lam.) de Wit (Fabaceae). It seems likely that there has been an established breeding population of one or both species for several years during a series of consecutive extremely mild winters since 1989. Because both butterflies have broad ranges and disperse readily throughout the Caribbean (Smith et al. 1994) and have recently become established in Florida, it is likely that these butterflies arrived in west coastal Florida by natural dispersal. Lee and Jackie Miller have seen *E. angelia* every year since, through the spring of 1996, and Anderson has taken both species in Pinellas County, so apparently both species are still firmly established. The butterflies certainly are not limited by their anacardiaceous foodplant, which ranges to near Clearwater in northern Pinellas County, and both species should be sought elsewhere in southwestern Florida.

Lee and Jackie Miller also observed a specimen of *Dryas iulia largo* Clench on 28 February taking nectar at *Citrus* flowers. It was captured, found to be a ragged male, and unfortunately released before the real significance of the record was realized, as *D. i. largo* was known previously only from extreme southern Florida (Kimball 1965). The Manatee County specimen was observed farther north in west coastal Florida than any previous record, although a recent sighting in Orlando by Deuerling (see Baggett 1993) would suggest that this is another species actively expanding its range, possibly during the recent warm winters.

If there is a moral to be learned from this tale, it is that one can never say with confidence that one knows everything about the distribution of butterflies in an area. Many species may expand their ranges when conditions are favorable only to have the ranges contract subsequently. It will be intriguing to see whether the populations noted here can persist after a cooler winter with several frosts. There are many examples in the literature of transient populations of animals from many parts of the world. Armadillos and opossums are well-known examples of such prior dispersals in North America, and we have ob-

served expansions and contractions of butterflies such as *Calpododes ethlius* (Stoll) and *Siproeta stelenes biplagiata* (Fruhstorfer) in Central Florida. Because of larval hostplant relations, we also must remember that larvae might inadvertently be transported with nursery plants from different areas within the state. However, the lycaenid records listed here were made long after the active growth period when exotic plants would normally be brought into Central Florida for sale in local nurseries.

We consider voucher specimens to be an absolute necessity in faunal survey studies in order to adequately determine the taxa represented in an area. Vouchers of *M. azia* and *E. angelia* discussed here have been deposited in the collections of the Allyn Museum of Entomology, Florida Museum of Natural History.

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REPRODUCTIVE ADAPTATIONS OF THE TASAR SILKMOTH, *ANTHARAEA MYLITTA* (SATURNIIDAE), TO EMERGENCE SEASON

Additional key words: ovary, coupling, fecundity, hatching, diapause.

Most insects survive periods of environmental stress by entering a state of diapause. The Indian tropical tasar silkworm, *Antheraea mylitta* Drury, completes two to three generations in a year (Sinha & Chaudhuri 1992), and in bi/trivoltine broods undergoes pupal diapause for a period of about six to seven months to overcome unfavorable environmental conditions (Dash & Nayak 1988, Kapila et al. 1991, Sinha & Chaudhuri 1992). Pupal diapause in this species normally terminates at the end of May and eclosion begins in June with the advent of rain (Sinha & Chaudhuri 1992). This is known as optimal seasonal emergence. However, in the diapausing brood a portion of the pupae hatch 1–2 months early, emerging in a presumably unfavorable climate before the rainy season (Kapila et al. 1991). The physiological/hormonal basis of this erratic eclosion remains unclear, although endocrine regulation of pupal diapause in other insects has been well documented (Browning 1981, Denlinger 1985). Daily patterns of insect behavior (e.g., locomotion, feeding, emergence, mating, oviposition, and hatching) are governed by daily cycles of temperature, humidity, and light intensity as well as by physiological events (Beck 1983, Ratte 1985, Ashby & Singh 1990). We report here on ovary morphology and reproductive behavior of “seasonally” and “unseasonally” emerged tasar silk moths.

One thousand diapausing *A. mylitta* pupae of each sex were observed as they emerged

TABLE 1. Emergence and reproductive parameters for seasonally and unseasonally emerged *Antheraea mylitta*. Asterisks indicate significant differences between seasonally and unseasonally emerged moths ($P < 0.05$, t -tests).

Parameters		Seasonal	Unseasonal
% Emergence			
	male	62.80	0.70
	female	67.90	0.90
	total	65.35	0.80
% Coupling			
	self	47.42	11.11
	mechanical	37.70	55.55
	total	85.12	66.66
Female moth weight (gm)*		6160.12 \pm 110.95	4015.50 \pm 210.97
Ovary weight (mg)*		3598.75 \pm 98.08	2092.50 \pm 55.87
Single egg weight (mg)*		10.05 \pm 0.10	8.07 \pm 0.13
Number of eggs			
	laid*	162 \pm 5	10 \pm 1
	unlaid	44 \pm 4	42 \pm 1
	total*	206 \pm 8	52 \pm 2
% Eggs			
	laid*	78.96 \pm 1.59	19.59 \pm 1.71
	unlaid*	21.04 \pm 1.59	80.41 \pm 1.71
Incubation period (d)*		8.55 \pm 0.15	7.50 \pm 0.20
% Hatching*		80.76 \pm 1.58	18.48 \pm 3.93
Average temperature ($^{\circ}$ C)			
	minimum*	26.80 \pm 0.31	23.10 \pm 0.28
	maximum*	30.36 \pm 0.26	32.97 \pm 0.24
Average relative humidity*		73.46 \pm 1.27	39.96 \pm 1.73

in 1991. These had fed previously as larvae on the leaves of *Terminalia arjuna*. Moths that emerged during March–April were considered “unseasonal” whereas those that emerged during June–July were considered “seasonal.” Emergence and mating percentage were recorded for each group. Moths were allowed to pair naturally for about three or four hours; adult females unable to mate were coupled manually. Subsequently, the moths were allowed to oviposit. Egg production was recorded by counting the number of eggs laid by females, and the number of unlaid eggs was determined by dissection. Ovary morphology was assessed after removing the whole system from the adult moth. Temperature and relative humidity were recorded throughout the observation period.

Table 1 shows variation in reproductive parameters in relation to emergence. Unseasonal eclosion was rare in comparison to seasonal eclosion, and the natural coupling percentage of unseasonally emerged moths was lower. Unseasonally emerged female moths had lower body weight, lower total ovary weight, lower single egg weight, and decreased egg production, egg laying capacity and egg hatching. Table 2 indicates that unseasonally emerged moths had smaller ovaries, ovarioles, and mature eggs. Unseasonally emerged

TABLE 2. Physical dimensions of ovary, ovarioles and mature eggs (after laying) of unseasonally and seasonally emerged *Antheraea mylitta*. Significant differences between seasonally and unseasonally emerged moths existed for all traits measured ($P < 0.05$, t -tests).

	Ovary		Ovariole		Mature eggs	
	Length	Width	Length	Width	Length	Width
Seasonal	55.67 \pm 0.54	14.67 \pm 0.27	84.25 \pm 0.58	3.07 \pm 0.03	3.04 \pm 0.04	2.53 \pm 0.02
Unseasonal	42.33 \pm 1.19	11.33 \pm 0.54	65.12 \pm 0.61	2.50 \pm 0.02	2.54 \pm 0.04	2.19 \pm 0.04

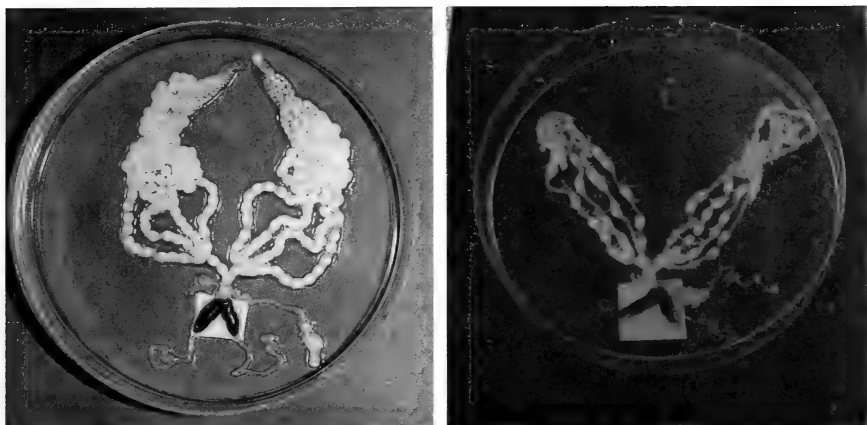


FIG. 1. Ovaries of seasonally (left) and unseasonally (right) emerged *Antheraea mylitta*.

moths also frequently had oocyte-free zones when compared to seasonally emerged moths (Fig. 1).

Temperature fluctuated more during March–April than during the months of June–July, and relative humidity was lower in March–April. Variation in ambient environmental factors may be responsible for some of the observed differences in reproductive biology in *A. mylitta* (see e.g., Messenger 1964, Hagstrum & Leach 1973, Beck 1983, Sidibe & Lauge 1977, Ratte 1985, Ochieng'-Odero 1991), but we do not yet know why pupal diapause occasionally terminates early in this species. Biogenic amines have been implicated in the regulation of development, especially in diapause induction and termination (Puiroux et al. 1990), and our own unpublished observations suggest that octopamine plays a major role in termination of pupal diapause in *A. mylitta*. Unseasonally emerging tasar silk moths are not being exploited commercially at present.

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BOOK REVIEWS

MARIPOSAS DE CHIAPAS, by Roberto G. de la Maza E. and Javier de la Maza E. 1993. Gobierno del Estado de Chiapas. Distributed by Montes Azules, Camino Real a Xochimilo No. 60, Tepepan Xochimilo 16020, Mexico DF, Mexico (email: bfly@sar.net). 223 pp., 152 color plates. Hardcover, dustjacket, 21.5 x 28.5 cm, ISBN 968-6258-34-5. \$60 US (postpaid).

Chiapas holds a special place in my heart—my first experience of the neotropics was a month-long unstructured tour of the state. I return every few years to recapture the excitement I felt during that month-long adrenaline rush, and Chiapas never fails me. It is a land of contrasts, culturally and biologically the richest state in one of the most diverse countries in the world, yet its neglected economy and ecologically abused highlands contribute to an air of depression. Its habitats run the gamut: from lowland rain forests and swamps, through the rich forests of the lower elevation hills, and upwards to the highland deserts, oak/pine forests, and tropical cloud forests along mountainous ridges. Its highland butterflies include species more familiar to Canadians, such as *Nymphalis antiopa*, *Papilio polyxenes*, and *Colias eurytheme*, whereas in the lowlands, classic Neotropical genera abound, such as *Morpho*, *Memphis*, and *Parides*. Thus, it is fitting that this marvelous volume is defined by its contradictions, characterized in many respects by what it is not rather than what it is. It is *not* an identification guide, but it is a picture book with over 100 mostly superb photographs of butterflies in their natural habitats. It is written for local consumption as a general introduction to butterflies, and yet it contains a storehouse of natural history and distribution information that will be used throughout Central America and beyond. It is not, however, an easy book from which to extract this valuable information, and most of the species-specific information is presented in tabular format.

In the tradition of the family's *Mariposas Mexicanas* (R. de la Maza R., 1987, *Mariposas Mexicanas*, Guía para su Colecta y Determinación, 302 pp., 67 color pls.), the current volume features not just butterflies, but the context in which they occur, devoting 170 pages of text and photographs to historical and ecological context. The book opens with an brief overview of butterfly life history and ecology, but quickly focuses on Chiapas ecosystems and biogeography. The bulk of this introductory section details the historical context that produced this volume—the significant field collectors involved, and the interesting history of involvement of the entire de la Maza clan with Chiapas butterflies. Have no doubt about it, this book is as comprehensive an effort as has ever been mounted in Central America. The authors live in Chiapas, and this volume has been an obvious labor of love for many years. The field work and experience that underpins this volume is unequaled for Central America.

The heart of the book is the chapter entitled 'La fauna de mariposas chiapanecas,' which includes a powerful trip through the major ecological and faunal butterfly communities of Chiapas. First, the authors de-construct faunal communities into those of disturbed habitats and those of 'stable ecosystems'—a division that literally separates species that thrive in highly disrupted landscapes from those that require relatively undisturbed habitats. These two categories are each divided further, the disturbed fauna by altitude, the habitat-restricted fauna by broad vegetational cover types, which seem to be strongly influenced by altitude, rainfall, and biogeographic affinities. Each faunal community is discussed relative to the primary factors that influence the habitats found within it, and each discussion is illustrated with excellent maps, habitat photographs, and some excellent photos of the more interesting butterflies found there, such as those that are the most habitat restricted or which are characteristic of the fauna. This section includes many photos of species that are rarely seen. This chapter continues with a curious attempt to group butterflies based on broad evaluations of color patterns and which portion of the habitat they use. For example, 'Patrón banda oblicua' (which I broadly translate as 'butterflies with an oblique band through their forewing,' mostly nymphalids but including some metalmarks and skippers) are found primarily in the sub-canopy of forest communities. Although there may in fact be some truth to these generalizations, the exceptions drive you mad, and the

end result depends to no small degree on difficult decisions of where to place a given butterfly species in these 21 pattern groups. The subjective quality of the groups allows the reader considerable latitude to move species around among the groups to fit one's preconceptions, although the arrangement is certainly thought-provoking. This chapter ends with an overview of butterfly life histories and the conservation status of the Chiapas fauna as well as the threats to biodiversity that face the state.

The final chapter is a beguiling overview of butterfly classification, which opens with a comparison of the classification system used in the village of Tzeltal for the conspicuous kinds of butterflies (large, small, white, blue, etc.) relative to traditional Linnean classification. The remainder of the chapter is devoted to an overview of the families and subfamilies of butterflies in Chiapas. Although most taxonomists may fret about the classification followed in this book, my opinion is that it doesn't detract from the utility of the volume.

The appendices are what I find most interesting. Appendix II is a simple listing of 52 species that are in danger of extinction in Chiapas. The list includes a few species with which I am familiar, but most of these species I have never encountered in the state. Because this is simply a list of species, it is difficult to determine if these species are truly imperiled with identifiable threats, or are simply very rarely encountered. I suspect that the list includes both, but generic threats to biodiversity abound in Chiapas, and I have no doubt that deforestation of highland and tropical forests threaten many of the locally distributed species.

In my view, Appendix I is the technical core of this book—a 34-page listing of the 1,194 species known from Chiapas. No listing like this from the Neotropics will ever be 100% complete, but certainly this is the best so far published for the region. (There are at least two additional skippers from the state that I am aware of, and I am sure other readers will find records in their collections, too, although the additions to be made are certainly minor.) This appendix is the first complete faunal list, including all butterfly families, from a discrete Central American region, so this information is illuminating.

But Appendix I is more than just a list of species—five columns of data are included for each. The first column divides the state into nine zones of distribution, and lists the status of each species and subspecies in each zone (several taxa are represented by two subspecies in Chiapas, thanks to mountainous terrain that effectively divides the lowland tropical ecosystems of the state). Status within each of these regions is coded as 'established, present, extinct, dubious, or requires confirmation,' thus providing some insight into each species' abundance. Next is a series of codes that tell you to which of the faunal group(s) the butterfly belongs. Because the distributions of these faunal groups are mapped, this information can be combined with the nine zones of distribution to develop a pretty refined guess as to the actual (or potential) range of each species within Chiapas. The third column's codes refer to that system of wing-coloration and habitat-use grouping that I mentioned previously. I have absolutely no idea what column 4 stands for—it is labeled PC and I simply can't find any information about it or about the codes listed under this heading. I am not sure if the explanation got dropped during editing or if my broken Spanish prevents me from finding this information. Either way, this is a vexing problem. The final column presents the altitudinal range from which the species is known (which can be added to columns 1 and 2 to further refine range estimates). In summary, this valuable appendix provides a wealth of information and I find myself referring to it on a regular basis.

I cannot resist the urge to make a simple faunal comparison between Chiapas and Costa Rica. In total, Chiapas has fewer species of Nymphalidae, Pieridae, and Papilionidae than does Costa Rica: ca. 450 species compared to Costa Rica's ca. 550 (P. J. DeVries, 1987, *The Butterflies of Costa Rica and their Natural History: Papilionidae, Pieridae, Nymphalidae*, Princeton University Press, 327 pp., 50 color pls.). But what this volume sharply defines is the magnitude of the butterfly fauna not covered by DeVries—Lycaenidae, Riodinidae, and Hesperidae, namely, the two-thirds of the butterfly fauna that is more difficult to adequately inventory and identify. In this regard, the Chiapas volume truly fills a gap in our knowledge of Mesoamerican butterflies and allows us to better ponder the realities of butterfly diversity in the region.

So, do I recommend this volume? Unequivocally, yes. It has been quite a while since I

purchased a book in this price range that did not disappoint—usually such books are all fluff and no content. At twice the price, *Mariposas de Chiapas* would be a bargain.

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CARCASSON'S AFRICAN BUTTERFLIES: AN ANNOTATED CATALOGUE OF THE PAPILIONOIDEA AND HESPERIOIDEA OF THE AFROTROPICAL REGION, edited by P. R. Ackery, C. R. Smith, and R. I. Vane-Wright. 1995. CSIRO Publications. ix + 803 pp., 300 black-and-white photographs. Hardcover, 27.5 x 21.0 cm, ISBN 0-643-05561-4. \$150. (In North America, order from ISBN, 5602 NE Hassalo Street, Portland, OR 97213-3640.)

Upon first glimpse of the title, one may ask: "Who is this fellow Carcasson, and which are *his* African butterflies?" The answers to these questions (and many others) are found on the first few introductory pages of this handsome book. Bob Carcasson was an English-born entomologist who spent a considerable portion of his highly productive career in Africa, studying the Lepidoptera of that continent. A draft manuscript prepared by Carcasson over 25 years ago was the nucleus upon which this extremely thorough treatment was built. The final product is the result of the masterful editorship and knowledge of three outstanding British lepidopterists—P. Ackery, C. Smith, and R. Vane-Wright.

This annotated (and illustrated) catalogue represents the first comprehensive treatment of the butterfly fauna (Papilionoidea and Herperioidea) of any large tropical region. Carcasson defined the Afrotropical Region (equivalent to the Ethiopian Region of other authors) on the basis of zoogeography rather than political boundaries; hence, the butterflies of North African countries such as Morocco, Libya, and Egypt are not included. The catalogue includes over 3600 species representing a whopping 20% of the world's butterfly fauna. (Among the major faunal realms, the Afrotropical Region supports the third richest butterfly fauna, following the Neotropical with approximately 7900 species and the Oriental with approximately 4100 species.) A representative of each of the 300 genera treated is illustrated in a life-sized, black-and-white photograph at the beginning of each generic treatment. The catalogue includes all generic, specific, and infraspecific names of the butterflies of the region, organized in a highly usable fashion. Families, subfamilies, and genera are arranged phylogenetically, with species names arranged alphabetically under each genus. There are about 14000 names in the catalogue, including all described species, synonyms, forms, etc.

Under each species citation is a reference to the original description and brief notes on its distribution. Where known, information on host plants and other biological features is summarized.

The text of the book begins with a brief introduction and a section on general butterfly biology in the Afrotropical Region. Next there is an extensive gazetteer, which is particularly useful given the instability of place names in Africa over the past 50 years. Following is a section on biogeography that is an updated and slightly modified version of one of Carcasson's most influential publications—A *preliminary survey of the zoogeography of African butterflies*. The next 620 pages are dedicated to the catalogue itself. The book includes a comprehensive index and an up-to-date bibliography on African butterflies.

There is little to criticize in this beautifully produced work. My only complaint is that there seems to be a considerable amount of wasted space. Numerous pages are only half-filled with text, and a few have only two or three lines. (This is an extremely trivial complaint for such a large work.)

In summary, *Carcasson's African Butterflies* is an extremely thorough, well-organized, highly usable catalogue of the butterflies of the Afrotropical Region. The introductory ma-

terial and illustrations enhance considerably its usefulness and value. The book should have a wide appeal to professionals and amateurs interested in any aspect of the butterflies or zoogeography of the Afrotropical Region.

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CORRECTION TO VOLUME 51

In the General Note by A. K. Sengupta and A. A. Siddiqui, "Effects of gene-environment interaction on silk yield in *Antheraea mylitta* (Saturniidae)," which appeared in 51(1):95-97, the captions for both Tables 1 and 2 carry the incorrect taxon. The name *Bombyx mori* appears erroneously instead of *Antheraea mylitta*.

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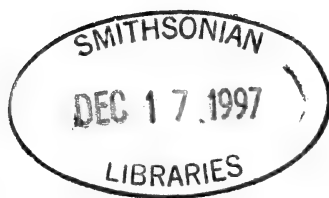
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Cover illustration: the Large Yellow Underwing, *Noctua pronuba* L., a newcomer to Connecticut during 1993, and a "missing person" in the recent Peterson's *Field Guide to Eastern Moths*. This palearctic noctuid has rapidly expanded its range and population size throughout eastern North America since its introduction into Canada nearly two decades ago. Original pen and ink drawing by John Himmelman, 67 Schnoor Road, Killingworth, Connecticut, 06419, USA.

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MALE MATE-LOCATING BEHAVIOR AND YEARLY POPULATION CYCLES IN THE SNOUT BUTTERFLY, *LIBYTHEANA BACHMANII* (LIBYTHEIDAE)

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ABSTRACT. This paper describes mating behavior and seasonal changes in population size in the snout butterfly, *Libytheana bachmanii*. At a central Arizona study site, we found a dramatic peak in the abundance of snout butterflies in late May and early June, with a smaller peak in the fall. Both peaks lasted several weeks and were separated by periods when few or no adult butterflies were found. Males are classic patrollers and search for females in and around the larval foodplant, desert hackberry (*Celtis pallida*). Courtship is like that of many other butterflies, with no distinctive displays by the male or female. We compare these results to those for the desert hackberry butterfly, *Asterocampa leilia*, which uses the same larval foodplant but has very different mate-locating tactics and, as some hypotheses predict, relatively stable and medium density populations from season to season.

Additional key words: desert hackberry, central Arizona, courtship.

The behavior of male insects at mate encounter sites varies along several axes. These include the time of day males visit sites, the duration of visits to a site, and whether males defend sites (Thornhill & Alcock 1983). Ultimate explanations for differences within and among species in these components of male behavior at encounter sites invoke ecological variables such as population density and encounter site size and distribution (Thornhill & Alcock 1983, Bradbury 1985). A special opportunity to study the ecological correlates and causes of mating systems arises when two or more species of similar size use the same encounter

sites but differ in mate-locating tactics. In these situations, certain features of habitat and scale are naturally controlled, which permits a focus on differences in other factors such as population density that may have influenced the evolution of male mate-locating behavior.

In the upper Sonoran Desert of western North America, two butterfly species similar in size occupy the same locale and use the same larval food plant, desert hackberry (*Celtis pallida* Torrey; Ulmaceae). These butterflies appear to exhibit striking interspecific differences in male mate-locating behavior and in population dynamics. In one of the species, the desert hackberry butterfly, *Asterocampa leilia* (Edwards) (Nymphalidae), males are classic "perchers" (Scott 1974) that occupy and defend perch sites on or next to the larval food plant (Austin 1977, Rutowski & Gilchrist 1988, Rutowski et al. 1991). A male may occupy the same site for several mornings. In contrast, males of the other species, the snout butterfly, *Libytheana bachmanii* Strecker (Libytheidae) have been described as perchers by some (Scott 1986) and "patrollers," that conduct aerial searches within hackberry trees but do not occupy or defend perches, by others (Rutowski 1991).

Selection should favor males that patrol when the costs of site tenacity and defense outweigh the benefits (Brown & Orians 1970, Rutowski 1991). This should occur when population densities are extremely high or low. At high population densities the rate of interactions with intruders should place a high cost on site defense; at low population densities, the low rate of female arrival will yield low returns from site defense. Intraspecific switches from perching to patrolling have been related to increases (Alcock & O'Neill 1986, Wickman 1988) and decreases (Wickman & Wiklund 1983) in population density in other butterflies. The snout butterfly is notorious for undergoing large population explosions ("usually in late summer" Bailowitz & Brock 1991; "emigratory flights of millions of butterflies" Pyle 1981; Scott 1986), but the timing and duration of these events and population sizes between outbreaks have not been quantitatively documented. Populations of *A. leilia* are apparently subject to much less fluctuation (Rutowski et al., 1996).

To determine if an association exists between population characteristics and male behavior, we quantified population dynamics and features of the male and female behavior in *L. bachmanii*. Here we address the following questions: (1) what annual changes occur in the population size of this species; (2) what search tactics do males employ, and how do they differ from those of *A. leilia*; (3) what is the nature of courtship in this species; and (4) what is the mating history of individual females? Finally, we compare our profile of *L. bachmanii* with previous data on *A. leilia* and relate this information to hypotheses about the role of population density in the evolution of male behavior at mate encounter sites.

METHODS

Study site. We studied *L. bachmanii* at Round Valley in the Sycamore Creek flood plain, approximately 70 km NW of Phoenix, Arizona. The primary vegetation at this site includes shrubs and low trees, such as desert hackberry, mesquite (*Prosopis* spp.), catclaw (*Acacia greggii* Gray; Leguminosae), and paloverde (*Cercidium* spp.). The observations reported here were made from 1987 to 1995.

Census techniques. To assess yearly and daily changes in population size of *L. bachmanii*, we selected and mapped a 270 m census trail in the study site. The trail ran through a stand of hackberry trees and was used previously to census *A. leilia* populations (Rutowski et al., 1996). On each census, an observer walked the entire length of the route and recorded the location and behavior (perched or flying) of each *L. bachmanii* individual (males and females) seen on the census route. We tried to complete each census within 10 to 15 min to avoid counting moving individuals more than once; the cost of this approach was that we could not reliably distinguish males and females on the wing, so they were not scored separately. We censused the population in this way on sunny days every seven to 14 days during the flight season and once a month at other times, for a total of 40 days, from March 1993 to October 1994. On 35 of these days we ran four hourly censuses, from 0900–1200 h (MST). The other five days were during periods when no butterflies were found, so we ran only two or three censuses. At the end of each census, we measured the air temperature in the shade at 1 m above the ground.

Behavioral observations. Intrasexual and intersexual interactions were described from field observations. All interactions began when a male approached a conspecific. We recorded the durations of interactions from when an approaching male arrived within a few cm of the other individual until the interacting pair separated for the last time. Also, for a sample of perched males, we measured the height of each occupied perch. Observations and video records of field interactions between males and virgin females (reared from larvae collected in the field) of *L. bachmanii* were used to develop the description of courtship. To estimate mating frequencies of females, we dissected the females that had been collected at random and freeze killed during May, June, and July 1994. The abdomen of each was opened under insect Ringer's solution, and the number of spermatophores in the bursa copulatrix counted.

Tenure in hackberry trees. We attempted to determine if males behave differently in hackberry trees than they do in other trees. We selected a hackberry tree and a mesquite tree of similar size (about 3 m high and wide) that were representative of trees within the study site. An observer was stationed at each tree. At the same time, each observer

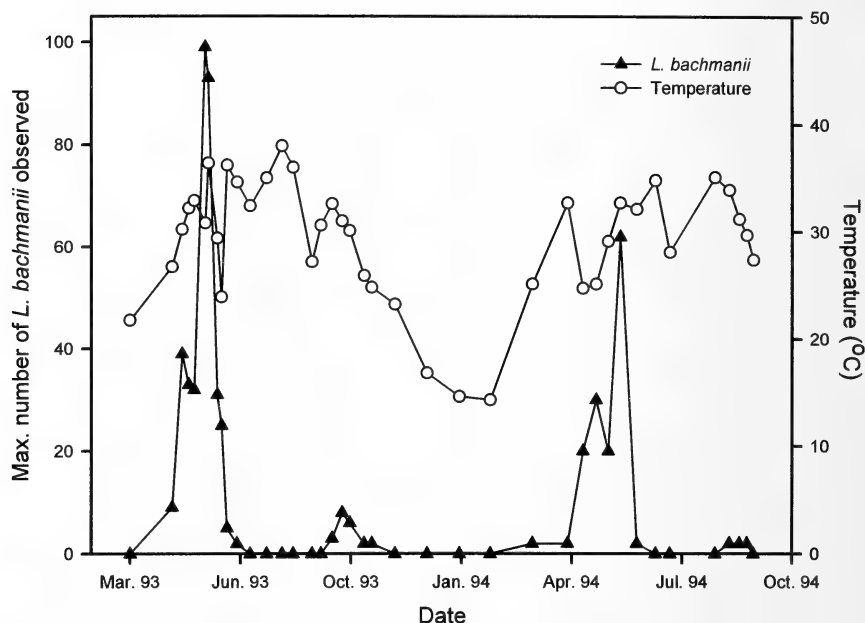


FIG. 1. Variation in the size of the *L. bachmanii* population and in the air temperature at 1 m with time of year. For each day on which we censused the population, the graph shows the maximum number of individuals observed on a single census and the temperature at the time of that census. *L. bachmanii* abundance is dependent on season but not on temperature (see text for details). This figure includes data from five days in which only two or three censuses were run and no butterflies were seen.

recorded the total time spent within the tree's perimeter for each male *L. bachmanii* that arrived at the tree. The data were collected on two sunny days in May 1986, using two different pairs of trees.

RESULTS

Population dynamics. The number of *L. bachmanii* seen along the census route on any given day fluctuated dramatically within each year (Fig. 1). On most days the maximum number of butterflies seen on any given census did not exceed 10 individuals; however, on three out of 40 census days we counted more than 60 individuals in at least one census. Flight seasons occurred at the study site twice each year: over six to eight weeks during May and June, and from four to six weeks during September and October. Peak population density was much greater during the spring flight season than in the fall. The average number of individuals observed on a day varied significantly with time of year (Kruskal Wallis test, $n = 40$ days, $P = 0.006$; Fig. 1). However, the average number seen on a day when the butterflies were active did not covary with air temperature at 1 m at noon on that day (Kruskal Wallis test, $n = 35$

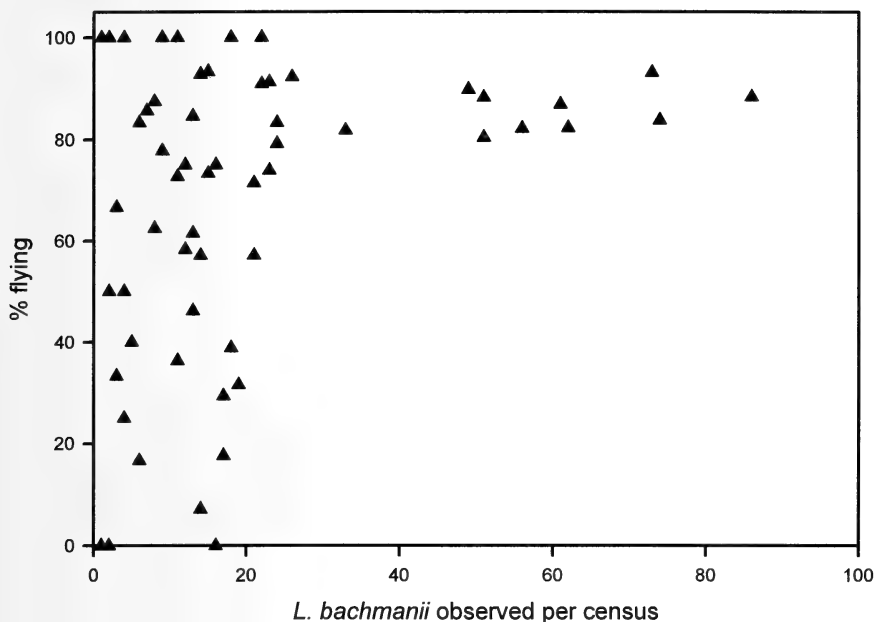


FIG. 2. The proportion of individuals seen in flight (rather than perched) as a function of population density ($n = 1222$). Butterflies that changed from flying to perching (or vice versa) while being censused not included.

days, $P = 0.437$). Although *L. bachmanii* are most abundant when ambient temperature is between 30 and 40°C, there were days on which these temperatures occurred but no butterflies were seen (Fig. 1).

Whether *L. bachmanii* were seen perched or flying during a census was related to the density of butterflies (Fig. 2). When we counted more than 20 butterflies along the census trail, at least 80% of them were flying. However, when counts were 20 or lower, the proportion of individuals in flight was variable, ranging from 0 to 100% of butterflies observed.

No consistent pattern of daily activity was found in the mornings (between 0900–1200 h). Time of day did not explain at all the number of adults seen on a census on days when the butterflies were active (ANOVA with time nested in date on log transformed counts during flight seasons, $df = 75$, $P = 0.999$). Moreover, we saw no consistent movement patterns that would lead us to describe these populations as migratory, as previous accounts have done (e.g., Pyle 1981).

Along the census route, snout butterflies were most commonly found near hackberry trees, their larval foodplant. When we divided the census route into 5 m segments and totaled butterfly sightings for each segment, we found that butterflies were not uniformly distributed along the trail (Fig. 3; $\chi^2 = 1034$, $df = 53$, $P < 0.0001$). Similarly, we found a non-

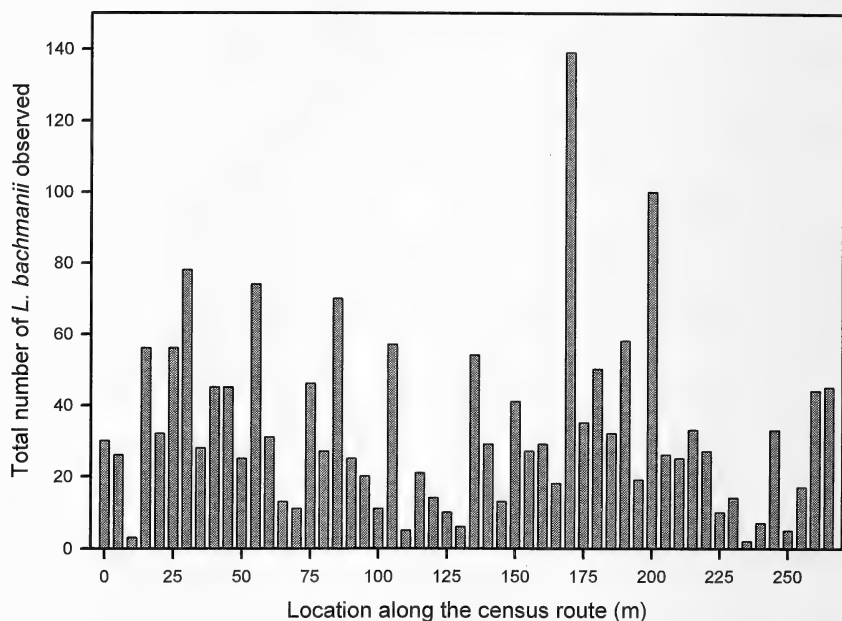


FIG. 3. Spatial distribution of *L. bachmanii* sightings ($n = 1797$) along the census route. The number observed on each 5 m segment is the total observed over 140 censuses on 35 days.

uniform distribution of hackberry trees along the trail ($\chi^2 = 36.9$, $df = 53$, $P < 0.05$). However, there was a significant, positive correlation between the number of *L. bachmanii* observed in each 5 m section of the census route and the number of hackberry trees in a section (Fig. 4; $r = 0.56$, $df = 53$, $P < 0.0001$).

Male searching behavior. Males were seen flying and perched in the study area, and flying males moved both within and among hackberry trees. Within hackberry trees, males moved slowly up and down close to branches and leaves. Perched butterflies were approached and inspected. Both flying and perching males approached and chased other butterflies (both conspecific and heterospecific) that flew nearby; however, at times two or three butterflies perched within a few centimeters of each other. Interactions with conspecific males in the spring flight period lasted an average of 14.6 ± 13.5 sec (median = 9.7 sec, range = 3.9–43 sec, $n = 8$). Males inspected heterospecifics for an average of 12.7 ± 10.3 sec (median = 7.3 sec, range = 2.8–36.2 sec, $n = 16$). The interaction durations were not significantly different (Mann-Whitney U test, $P > 0.9$).

Flying males spent significantly more time in hackberry trees than they did in mesquite (Fig. 5; Wilcoxon rank sum test, $n = 22$, $P = 0.001$).

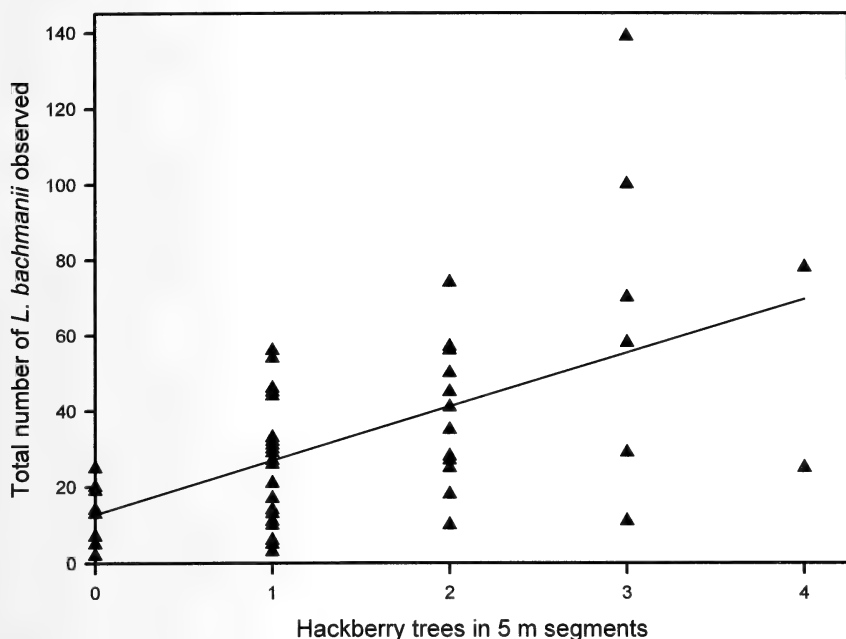


FIG. 4. The relationship between the number of hackberry trees and the number of *L. bachmanii* sightings in 5 m segments along the census route. There is a significant positive correlation between these variables ($n = 1797$, $r = 0.56$, $df = 53$, $P < 0.0001$).

Males moved through hackberry trees in an erratic, zigzag fashion. In contrast, their flight through mesquite trees was more direct, causing them to pass through the tree more quickly.

Males perched on exposed twigs and branches. Average perch height was 1.92 ± 0.31 m (median = 1.87 m, range = 1.5–2.5 m, $n = 17$) above the ground. The body of a perched male was oriented upwards with the wings closed or partially opened. The average time a male spent at a perch on a typical summer day was 77 ± 90.6 sec (range 3.4–430.3 sec, $n = 55$).

Courtship and mating behavior. Courtship leading to copulation began when a male approached a perched or flying female. A flying female was chased by a male until she alit on vegetation. A perched receptive female usually remained still with her wings folded as a male approached. The male then alit behind the female and moved alongside her with his head oriented in the same direction as hers. He then curled his abdomen toward the female, probing between her hindwings until he attained genital contact. After coupling, the male turned to face away from the female. During copulation, some females took flight, carrying the male with his wings closed, suspended head-down from her abdomen.

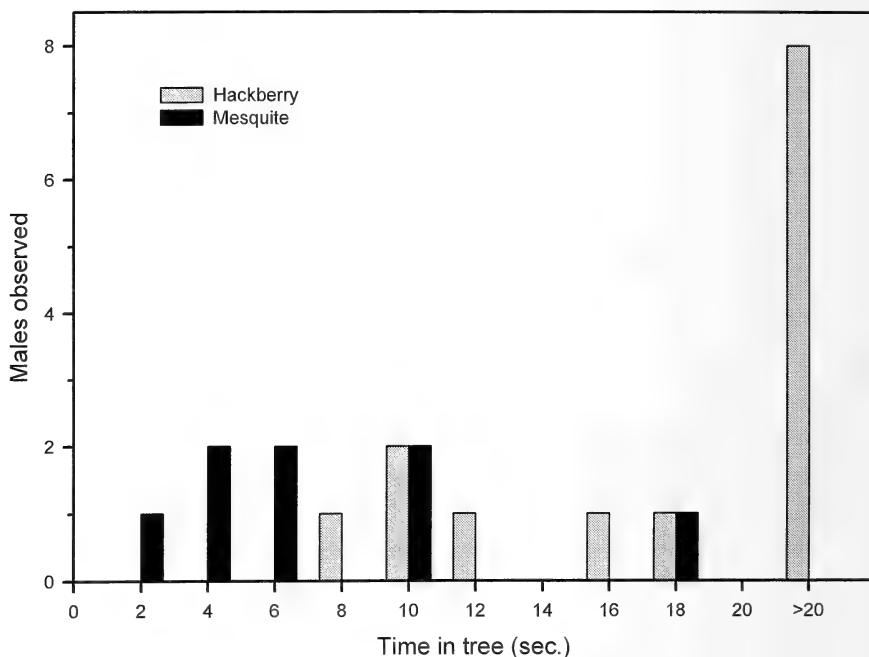


FIG. 5. Time spent by males in hackberry trees versus mesquite trees. See text for details.

Copulation ended when the pair uncoupled. Four pairs were found in copula, and the average time until they separated was 88.5 ± 40 min (range = 45–140 min, $n = 4$). During copulation the male passed a spermatophore to the female. The females collected for spermatophore counts were fresh to slightly worn in condition and carried an average of 1.28 ± 0.66 spermatophores ($n = 28$, range = 1–4 spermatophores). When females carried more than one spermatophore, one was roughly teardrop shaped, approximately twice as long as wide, and all others were partially or completely flattened and depleted. This suggests that matings do not occur in rapid succession. After copulation females flew about searching for oviposition sites. Eggs were laid singly, often on the end of sprigs of new hackberry growth.

Unsuccessful courtships lasted an average of 44.6 ± 79.7 sec (median = 42.3 sec, range = 23–78 sec, $n = 6$). In these interactions, flying females either did not alight, alit and fluttered their wings, or suddenly dropped toward the ground and alit. In the latter case, the male might search for the female, but he left after a brief time if he did not relocate her. Perched females may hinder males by spreading their wings and elevating their abdomens or by taking flight. On one occasion a male pur-

sued a female in direct upward flight for about 5 m. The chase lasted for less than one minute, until one of the butterflies was captured by a cliff swallow (*Hirundo pyrrhonota* Vieillot).

DISCUSSION

The major results of this study are as follows. First, the *L. bachmanii* population that we studied in central Arizona displays an explosive increase in numbers twice a year, especially in the late spring. The reasons for these dramatic changes are not known. Apparently the snout butterflies diapause once or twice a year, but the stage in the life history at which this occurs or why it occurs at these times are not known. One possible answer is that population cycles are tied to the phenology of the desert hackberry. Hackberry trees produce new vegetation after the rainy periods that occur regularly each winter and mid to late summer. The new vegetation may foster the development of the larvae.

Second, both males and females are found primarily in or near the larval foodplant. Females are seeking oviposition sites; males are seeking females. Our observations show that males entering hackberry trees change their behavior from direct flight to a zigzag searching of the vegetation. We conclude that males are seeking both newly emerged virgin females and previously mated females. Newly-emerged females are likely to be common in hackberry trees because the larvae pupate on the larval foodplant (pers. obs.). In addition, we have in several instances seen a male mated with a newly emerged female (wings still flexible) next to a pupal exuvium on hackberry. Males are also probably looking for previously mated females who are ovipositing but are ready to mate again. Spermatophore counts show that females will mate more than once. Use of the larval foodplant as the mate encounter site has been reported for other butterflies (Lederhouse et al. 1992, Rutowski & Gilchrist 1988).

Third, at the larval foodplant, males use primarily a patrolling strategy to locate females. Figure 2 suggests the incidence of a territorial strategy at low population densities; however, several observations argue against this. Males always show low interest in other males and little site tenacity. In addition, we never saw any male-male contacts that led to the spiraling aggressive interactions described for some territorial species (e.g., Baker 1972). Finally, males and females are not distinguished in Fig. 2, and temperature, which could also play a role, is not controlled. Even if we ignore these confounding variables, most individuals at all population densities are on the wing.

Fourth, although the snout butterflies are a worldwide family of only nine species reported to have diverged from other butterfly lineages at least 35 million years ago (Emmel et al. 1992) and have unique palpal and wing morphologies, their courtship and mating behavior are very

much typical of that reported generally for butterflies (Scott 1973, Silberglied 1978, Drummond 1984, Rutowski 1984).

Relationship between population density and male behavior at encounter sites. The documentation of the dramatic seasonal changes in population density in *L. bachmanii* provided here supports the hypothesis that population density is an important determinant of male tactics. Because population densities are usually extremely low or, for a brief period, extremely high, the costs of site tenacity and defense should outweigh the benefits. Patrolling has then evolved as the primary mate-locating tactic in this species.

The idea that population density is an important determinant of male behavior at encounter sites is further supported by comparing the results reported here for *L. bachmanii* with what is known of *Asterocampa leilia*, the desert hackberry butterfly. Males in this species also use desert hackberry as the mate encounter site. However, they occupy and vigorously defend perching sites on or next to hackberry trees where they sit and wait for females to fly by. In contrast to *L. bachmanii* and in support of the population density hypothesis, the population of *A. leilia* at the Round Valley site is relatively stable for a long period each year. On the same census route used in this study, we found an average of about 10 perching males from April to November (Rutowski et al., 1996). Compared with *L. bachmanii* their populations are at an intermediate level and relatively stable, which has, in our view, favored the evolution site tenacity and defense.

Meteorological variables have also been proposed to explain intra- and interspecific differences in whether males patrol or perch at encounter sites (Dennis 1982, Wickman 1985, 1988, Alcock 1994). However, in neither *L. bachmanii* (this study) nor *A. leilia* (Rutowski et al. 1994) have we seen any evidence that males switch from patrolling to perching or vice versa with changes in season, temperature, or time of day. Also, both species engage in their respective mate locating activities at the same time of the day. In summary, while this study implicates differences in population density to explain interspecific differences in male behavior, other nonmutually exclusive explanations such as temperature and predation will also need to be examined.

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RELATEDNESS AND GREGARIOUSNESS IN THE ORANGE-STRIPED OAKWORM, *ANISOTA SENATORIA* (SATURNIIDAE)

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ABSTRACT. Oakworm larvae live in groups and provide a convenient model system for the study of gregarious behaviors of caterpillars. Most caterpillar groups consist largely of related individuals, so the costs and benefits of gregariousness must be considered within the framework of kin selection. In this study, we use allozymes to estimate relatedness within 11 groups of 4th–5th instar larvae. Allozyme diversity was high in four marker loci, with an average heterozygosity of $H_{exp} = 0.376 \pm 0.029$ (SD) when frequencies were pooled over groups. We found a relatedness of $r = 0.31 \pm 0.056$, a relatively low value given that full-siblings show $r = 0.5$. The mean nearest-neighbor distance among plants was 4.34 ± 3.48 m, and among groups it was 5.25 ± 4.15 m. Within the framework of a mathematical dispersal model calibrated using observations of larval movement in the field, these values suggest that only about 4% of wandering larvae ever find new hosts, and that exchange is negligible among groups on different plants. Adult behaviors, either multiple mating or aggregation of egg clutches, are therefore probably responsible for the observed relatedness values.

Additional key words: caterpillar ecology, Lepidoptera, dispersal, group living.

Oakworm moths (*Anisota senatoria* J. E. Smith) are primarily known by the considerable destruction their gregarious larvae can cause to the foliage of oaks in eastern North America (e.g., Coffelt, Schultz & Wolf 1993). The larvae are brightly colored and easily manipulated in the field, making them excellent models for the study of communal behaviors of caterpillars.

Natural history data relevant to the communal behavior of *A. senatoria* larvae are available from recent studies to assess and control their impact as pests in suburban landscapes (Coffelt & Schultz 1990, 1993). Adults emerge in late June to early July and copulate diurnally (Ferguson 1971), and females lay clutches of 200–700 eggs on the undersides of oak leaves (Coffelt & Schultz 1990). Host plants in other families have been reported in the older literature (compiled in Teitz 1972), but these are probably erroneous (Ferguson 1971). Females are weak fliers and over 90% of the clutches are laid within 5 m of the ground (Coffelt

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& Schultz 1994). The larvae appear to be confined to older leaves (Lawson et al. 1982, Coffelt, Schultz & Banko 1993). The larvae feed gregariously, resting on stems and twigs and relocating to nearby (often higher) branches as defoliation proceeds (Coffelt & Schultz 1994). Mature larvae pupate in the soil beneath their host trees. Most populations are univoltine, but bivoltine populations occur in the southern portion of the range (Ferguson 1971, Coffelt & Schultz 1994).

In most non-eusocial insects studied, group-living is initiated when females lay clutches of eggs (e.g., the eastern tent caterpillar, *Malacosoma americanum* (F.) (Lasiocampidae) (Costa & Ross 1993); the willow leaf beetle, *Plagiodera versicolora* Laicharting (Chrysomelidae) (McCauley et al. 1988)). Group living may subsequently be promoted by larval behaviors that maintain and enhance gregariousness, as in *M. americanum* (Fitzgerald & Peterson 1988) and *Pryeria sinica* Moore (Zygaenidae) (Tsubaki 1981), or it may be maintained simply by the absence of larval dispersal from the oviposition site.

Several selection pressures may act simultaneously on group-living behaviors of larval insects. Factors acting against group living in caterpillars include greater risks of detection by predators (Morris 1972, Stamp & Bowers 1988) and parasitoids, increased cannibalism, and greater chances of intragroup competition via defoliation of the host plant (Tsubaki & Shiotsu 1982). Those favoring gregariousness include facilitation of feeding on tough host leaves (Ito et al. 1982; and suggested for early instars of *A. senatoria* by Hitchcock 1961), the sharing of silken trails and nests (Fitzgerald & Peterson 1988), enhanced thermoregulation at low air temperatures (Stamp & Bowers 1990a), and potentially greater effectiveness of defensive behaviors against parasitoid attack (Stamp & Bowers 1990b). Additional benefits of larval gregariousness include enhanced effects of chemical defenses (Tostowaryk 1972 for *Neodiprion* sawfly larvae) and warning coloration (Sillen-Tullberg 1990) for distasteful species, and selfish-herd effects mediated by predation, provided that predation is not too intense (Hamilton 1971). These selection pressures may change with age, influencing the degree of grouping and cooperation that is optimal for larvae of different ages (Cornell et al. 1987, McCauley et al. 1988, Costa & Ross 1993). Inasmuch as individuals in larval groups are likely to be related because of maternal oviposition behavior, the costs and benefits of gregariousness need to be interpreted within a kin-selection framework.

In this study, we use allozymes to assess relatedness within late-instar groups of *A. senatoria* larvae, and present results of a simple experiment on larval dispersal ability to assess its influence on relatedness. Other factors that may influence *A. senatoria*'s gregariousness, outlined above, will be pursued in separate studies.

MATERIALS AND METHODS

Fourth and fifth instar larvae of *A. senatoria* were observed on individual red oaks (*Quercus rubra* L.; Fagaceae) at the Girdham Road sand dunes in Oak Openings Metropark in Lucas Co., Ohio, on 9 September 1995. The site includes a mixture of mature, sapling, and seedling age classes on a sandy substrate, and larval groups were abundant and easily accessible on the smaller plants. Larvae were identified using the key in Ferguson (1971). Few groups were seen at heights >5 m, in agreement with Coffelt & Schultz (1994).

Relatedness. Eleven larval groups were arbitrarily chosen and from each, 15 individuals (or all individuals if <15 were present) were removed and frozen at -80°C . Tissue was sampled by shaving slices from the abdomens of the still-frozen larvae, taking care not to include gut contents. Starch gels were prepared using standard techniques (Porter & Matoon 1989). Seven loci were stained: glutamic-oxaloacetic transaminase (GOT-1, GOT-2), malate dehydrogenase (MDH-1, MDH-2), malic enzyme (ME), phosphoglucumutase (PGM), and phosphoglucose isomerase (PGI). Alleles were scored alphabetically by locus. Individuals with rare alleles were re-run in adjacent lanes to confirm their scoring, and unresolved individuals were re-run as well.

The relatedness statistic, r , describes the extent to which individuals within groups share alleles, beyond the degree to which alleles are shared with an 'average' individual in the population as a whole. Grafen (1985) provides an excellent discussion of the interpretation of relatedness statistics. Relatedness was calculated using equation 6 of Queller & Goodnight (1989), a method that accounts for sampling bias. All calculations were performed using a population genetic analysis program written by A. H. Porter, which is available upon request.

Dispersal. Larvae were tested to determine their dispersal and re-aggregation capabilities following disturbances. Four plants <2 m in height were found with larval groups ($n = 22, 4, 5, 6$) on them. Concentric circles with 1, 2, and 3 m radii were drawn in the sand around these plants and the branch containing the group was jolted to simulate the arrival of a potential vertebrate predator. The larvae dropped to the ground and their movement distances and directions were monitored at 2 min intervals for 10 min. These were converted to average movement rates to provide a rough estimate of the ability of larvae to move among plants. The circle was divided into four quadrats and movement direction was determined for each larva as the quadrat it occupied after 10 min. Larvae could disperse in any direction so circular statistics (Batschelet 1981) were used on these data to assess whether the larvae tended to move together.

TABLE 1. Allele frequencies (s.e.) of the pooled data. Sample sizes (n) indicate number of stainable individuals for each locus.

allele	GOT-1	MDH-2	PGI	PGM
n	107	153	158	142
A	0.009 (0.001)	0.761 (0.002)	0.066 (0.001)	0.025 (0.001)
B	0.944 (0.001)	0.239 (0.002)	0.025 (0.001)	0.056 (0.001)
C	0.047 (0.001)		0.051 (0.001)	0.486 (0.003)
D			0.725 (0.002)	0.419 (0.003)
E			0.133 (0.001)	0.014 (0.001)

Distances among hostplants and larval groups. To estimate the probabilities of larvae moving between plant or to new groups, hostplants and all larval groups within 2 m of the ground were first identified and mapped within a 50 × 100 m area. This area was chosen because it contained sufficient plants and larval groups for a statistical analysis, and it was set apart from other areas with infested plants. The map was constructed by creating a lattice of triangles with sampled plants at the vertices, then measuring the distances between plants; nine missing measurements were estimated from field notes and sketches. Under this system, the coordinates of a third point of a triangle can be found using simple geometry once the first two are established. The lattice was thereby converted to a Euclidean coordinate system by establishing the coordinates of the first two points along a north-south line (the first point is at (0, 0), the second is at (0, *d*), where *d* is the distance between points) and iterating through the lattice until all coordinates were calculated. The distances between any two lattice points can then be found directly using the Pythagorean relationship. All calculations were performed using a *Mathematica* notebook (v2.2; Wolfram 1991). This convenient method provides an explicit map of all points of interest on the site without the need for erecting a grid. The method readily yields the distributions of interplant and intergroup distances, information that is not obtainable using nearest-neighbor measurements.

We estimated the proportion of wandering larvae that find new plants from the geometry of the plants in the study area. The angle subtended by a plant at distance *d* is 0.2/*d* radians, and the proportion of a search circle that culminates in a plant is 0.1 $\pi^{-1} \Sigma d^{-1}$. When plant density is low, these proportions are rather small, and to provide a conservative assessment of the role of dispersal, we chose assumptions that overestimated the chances of concluding that a larva would find a new plant. We thus assumed a relatively constant heading for a searching caterpillar, and that any plant within 10 cm of its path would be detected. A constant heading is the best strategy for a searching caterpillar when plant density is low (Jones 1977). As this assumption is relaxed and the

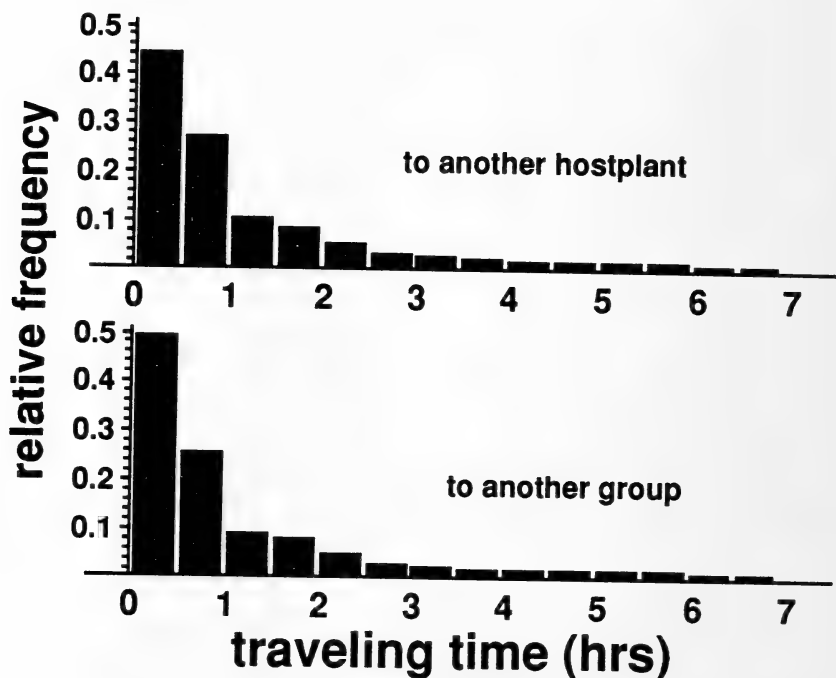


FIG. 1. Estimated distributions of traveling times for larvae successfully dispersing between plants, and between groups on separate plants. An additional 96% of larvae would not find plants at all.

propensity increases for larvae to change their heading during their search, they will wander along increasingly longer average paths before reaching new hosts. This is equivalent to increasing the distances between plants under a constant-heading search, and results in a somewhat lower probability of finding a new host. Dethier (1989) found that dispersing caterpillars tend to maintain relatively straight paths unless perturbed by obstacles. Our study plants were chosen for the relatively few obstacles in the sandy substrate around them, and this too may yield relatively generous estimates of dispersal capabilities. The value of 10 cm for the radius of detection was also chosen to be generous. When unaided by silken trails of conspecifics, other caterpillars species tested rarely showed orientation to hosts beyond 5 cm distance (Dethier 1959, Saxena & Khattar 1977, Saxena et al. 1977), though vertical stems (host or not) induced orientation in some species at 50 cm, even as far as 3 m (Doane & Leonard 1975, Roden et al. 1992). We did not adopt these higher values for three reasons. First, few larvae in our dispersal experiments returned to the source plant despite its close proximity, suggesting that such orientation capabilities are negligible in *Anisota senatoria*.

Second, plants of several non-host species were present in the study area in addition to young oaks, and orientation to these would tend to confound the search for appropriate hosts. Third, these higher values are based on orientation on a smooth substrate, and Dethier (1989) showed that as the substrate becomes more complex, search paths become more convoluted and larvae are increasingly apt to be influenced by encounters with obstacles at close range.

RESULTS

Genetic diversity and relatedness. The ME locus showed clear polymorphism, but because several alleles were difficult to resolve in heterozygotes, this locus was dropped from the analyses. MDH-1, the anodal locus, showed patterns that appeared to indicate polymorphism, but these were not repeatable and this locus was also omitted. GOT-2, the cathodal locus, showed no polymorphism. The remaining loci, GOT-1, MDH-2, PGI and PGM, showed sufficient polymorphism for use in the relatedness analysis. Allele frequencies of the pooled groups are shown in Table 1. The observed heterozygosity (s.e.) of the pooled groups was $H_{obs} = 0.386$ (0.022), with expected heterozygosity of $H_{exp} = 0.376$ (0.029). All groups showed polymorphism at >1 locus. Taken together, these results indicate that there was sufficient polymorphism available for a robust relatedness analysis.

The relatedness (SD) among late-instar *A. senatoria* group-mates was $r = 0.31$ (0.056), where the standard deviation is assessed by jackknifing over loci. This standard deviation drops to 0.033 if the variation is assessed over groups.

Larval dispersal capabilities. Oak plants at our site were separated by a mean (s.d.) nearest-neighbor distance of 4.34 (3.48) m. We found nearest-neighbor larval groups in our site to be separated by 5.25 (4.15) m ($n = 18$ groups), with the closest groups being on plants less than 1 m apart.

Fallen larvae rarely went back to the same plant. Upon falling, they moved at variable rates at relatively constant headings, averaging 1.5 (2.2) cm/sec. 32% of the larvae moved only little and thus did not leave the inner circle. There was no evidence that caterpillars took similar headings (Rayleigh tests, $P > 0.05$), indicating that they do not travel in groups once disturbed in this manner.

Based on our dispersal model, only 4% of the larvae that began searching (i.e., the 68% of larvae that traveled at least 1 m in the first 10 min) would ever encounter another host plant. This does not account for movement to plants off the grid, but these were mostly far enough away that the chances of a dispersing larva encountering them could be considered negligible. As noted in the Methods, this estimate is based

on assumptions that are already somewhat generous, and though it is low, it is still probably an overestimate. The low probability of finding a new host should therefore impose a strong limit on the exchange among larval groups on different plants.

We estimated the expected distribution of traveling times between plants by dividing each movement rate estimate by each distance between plants on the grid. Most of the fallen larvae that do find new plants (Fig. 1) would arrive there within the first hour (mean = 62 ± 78 min), and almost all successful larvae would find a new plant within 4 hr. Because of the spatial relationships among plants with and without larvae, approximately 65% of these new plants would already have larval groups, so the distribution of traveling times among groups (mean = 57 ± 75 min) is similar to that among plants (Fig. 1). Traveling time to new plants thus does not appear to be limiting exchange among groups, at least for the 4th and 5th instar larvae we studied. Larvae may also disperse of their own accord (Coffelt & Schultz 1993), whereupon they could expect to find suitable plants, and possibly join other groups, with similar probabilities and within similar time frames.

DISCUSSION

The degree of relatedness is moderate, well below the $r = 0.5$ value expected if larvae were always full siblings, but above the $r = 0.25$ level expected from half-sibs. This relatedness value is high enough to have strong effects on the realized costs and benefits of the gregarious behaviors of the larvae (Hamilton 1964). There are several ways that this level of relatedness could be realized, and these may be divided among behaviors of the ovipositing females and the subsequent behaviors of their larvae.

Larval behaviors that may reduce intragroup relatedness include active wandering to new groups during foraging bouts, as seen in *Malacosoma americanum* (Costa & Ross 1993), and inadvertent dispersal to new groups after falling off the host plant, as seen in *Hemileuca lucina* (Stamp & Bowers 1987). At Oak Openings, smaller plants with larval groups were often badly defoliated, and some had been abandoned by larvae. In some cases, we found small groups on plants with no evidence of the usual molt skins left by earlier instars, and these groups were adjacent to abandoned, defoliated plants. Even though host plants were relatively close together by human standards (4.34 m nearest neighbor distance), the distances remain formidable for wandering caterpillars, and only about 4% were likely to encounter new hosts. Plants with larval groups were still further apart, at 5.25 m, and we expect only a negligible proportion of larvae to be exchanged among them. This implies that the reduction in relatedness below $r = 0.5$ on the small,

isolated plants in our study is attributable more to the behaviors of adult parents, rather than to wandering by the larvae. However, intergroup exchange and coalescence in *A. senatoria* may be much more likely among clutches laid on the same plant, as seen in *Malacosoma* (Costa & Ross 1993). We would also expect it to be more pronounced at high density and later instars, when the defoliation rate is highest and larvae are forced to wander, and when larvae are big enough to travel at the rates we observed.

Adult behaviors that would reduce relatedness, not addressed in this study, include multiple mating with sperm-mixing that would result in broods of mixed full- and half-sibs (Wade 1982, 1985, McCauley & O'Donnell 1984), and the aggregation of egg clutches onto the same plant by different females (Wade 1985). These behaviors would be less effective in reducing relatedness to the extent that related adults mated or aggregated their clutches (Wade 1985). Of course, parental behaviors would influence the degree of relatedness and gregariousness initially displayed by larvae, but should not create subsequent changes in gregariousness associated with larval age.

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BIOLOGY OF THE BLACK-ANTENNA RACE OF *PHYCIODES* *THAROS THAROS* (NYMPHALIDAE) IN ONTARIO

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ABSTRACT. The black-antenna race of *P. tharos tharos* (Drury) occurs north to the Canadian zone of the Ottawa valley, far beyond the Carolinian or Upper Austral range limit previously indicated for the species. It is also reported for the first time from northern New York State and Quebec. The northernmost colonies are restricted to alvars or old pastures over limestone, but hay field and old field mosaics, dune slacks and prairies on sandy soils are utilized farther south. The foodplant at the northernmost sites was *Aster ciliolatus* based oviposition in the field and subsequent rearing in the laboratory. Available evidence suggests that the black-antenna race of *P. tharos tharos* may have invaded the Ottawa valley over the past five years: it is now widespread but local in southern Ontario, having been found in 65 locations. The flight period extends from late May to late October and is essentially continuous at some locations.

Additional key words: oviposition, foodplants, *Aster ciliolatus*, habitat, flight period.

Recent books (e.g., Scott 1986a, Opler & Krizek 1984, Opler & Malikul 1992) and monographs (Scott 1986b, 1994) follow Oliver (1980) in splitting *P. tharos* into two entities: the northern *P. cocyta* (Cramer) (= *P. selenis*, *P. pascoensis*, *P. morpheus*) and the more southern *P. tharos tharos* (Drury). Unfortunately, ecological and distributional data on the two species are confused because they previously were treated as one, and it is often unclear to which species certain information applies. The purpose of the present work is to provide ecological, distributional, and behavioral data for the black-antenna race of *P. tharos tharos* (subsequently referred to here simply as *P. tharos*) in Ontario, and update the otherwise comprehensive information available in the Ontario Butterfly Atlas (Holmes et al. 1991) and the annual summaries of the Toronto Entomological Association.

MATERIALS AND METHODS

Because females of *P. tharos* are often morphologically inseparable from those of *P. cocyta* and *P. batesii*, only males were used to develop distributional data. Males of the black-antenna race of *Phyciodes tharos tharos* were distinguished from *P. cocyta* males by the following characters in order of importance: (1) unscaled portions of the tip of the antenna (nudum) being all black or mostly black (black border and lattice with brown steps) instead of uniformly brownish-yellow, yellow or orange; (2) antennal clubs mostly club-shaped rather than elongate; (3) postmedian black line on upper hindwing extending through all or most cubital and medial cells rather than lacking in two or more cells; (4) median black band crossing upper forewing mostly well developed; (5) forewing 14–16 mm from base to apex instead of 16–18 mm; and (6)

marginal crescent patch on underside of hindwing dark brown instead of tan. Although a relatively small, multi-brooded race of *Phycioides* with yellow or brownish-yellow nuda, best referred to *P. cocyta*, occurs in parts of Ontario and New York state, this differs from the evidently more western orange antenna race of *P. tharos* in having the black lines on the upper wings less well developed. Only specimens having black antenna were accepted as the black-antenna race of *P. tharos*, but some variation was permitted in the other characters. However, the suite of characters associated with black antennae held together quite well. Black antennae were generally associated with well developed black lines on the upper wings for example, the most notable exception being a specimen at LEM from Laval (discussed below).

Collections examined included those at Agriculture Canada in Ottawa (CNC), the Royal Ontario Museum in Toronto (ROM), the University of Guelph (UG), Lyman Entomological Museum at Ste. Anne de Bellevue (LEM), and the University of Western Ontario (UWO). Members of the Toronto Entomological Association reporting *P. tharos* in recent season summaries (e.g., Hanks & Hess 1992, Hanks 1993, 1994, 1995) were contacted to confirm reports; their private collections were checked for other records of *P. tharos*. The map was produced using Quikmap version 2.5 (ESL Environmental Sciences Ltd., Sidney, British Columbia). Data for male *Phycioides tharos tharos* examined in institutional collections are as follows:

NEW YORK: Stony Point, 20 Jul 1995 (CNC); Chaumont, 2 Sep 1995 (CNC); Lockport, 11 km E, 14 Sep 1995 (CNC). **ONTARIO:** St. Davids, 23 Aug 1930 (UWO), 1 Aug 1932 (CNC); Brighton, 3 Aug 1932 (CNC); Fort Erie, 6 Aug 1948, 7 Aug 1948 (CNC); Marmora, 25 Jul 1952 (CNC); Ancaster, 26 May 1952 (CNC); Simcoe, 27 May 1953 (UG); Pottageville, 5 Sep 1955 (ROM); Unionville, 1956 (ROM); Don Valley, Toronto, 21 Jun 1958, 31 May 1958 (ROM); Dunn Twp., 27 Jul 1958, 1 Aug 1958, 16 Aug 1959, 18 Aug 1959, 16 Aug 1960, 29 Aug 1962 (UWO); Toronto, Don valley, 10 Jun 1959, 9 Aug 1959 (ROM); Orillia, 25 Jul 1959 (ROM); Toronto, Willowdale, 5 Jun 1960 (ROM); St. Catharines, 13 Sep 1961 (UG); Long Point, 25 May 1963 (ROM); Chaffey's Locks, 17 Jul 1963, 22 Jul 1970, 28 May 1971, 23 May 1974 (ROM); Dunnville, 22 May 1965 (ROM); Rondeau Park, 12 Jul 1965 (ROM); Wainfleet, 31 May 1969 (CNC); Oakville, 6 Jun 1976 (UG); Dundas, 21 Jul 1981 (UG); Aberfoyle, 10 Jul 1983 (UG); Vienna, 22 Aug 1987 (UG); 4 km W Dwyer Hill Siding, 22 Jul 1995 (CNC); Flood Rd., Rideau Twp., 22 Jul 1995 (CNC); 1 km W Metcalfe, 22 Jul 1995 (CNC); 2 km W Metcalfe, 22 Jul 1995 (CNC); 5 km N Metcalfe, 29 Jul 1995 (CNC); Huycks Bay, 9 Jul 1995 (CNC); Presqu'île Park, 15 Jul 1995 (CNC); Bells Corners, 30 Jul 1995 (CNC); Batawa, 7 Aug 1995 (CNC); Kemptville, 1 Sep 1995 (CNC); Queenston, 14 Sep 1995 (CNC); Almonte, 5 km NE, 3 Sep 1995 (CNC); Dwyer Hill Siding, 5 km SE, 4 Sep 1995 (CNC); 2.5 km SW Phragmites fen near Dwyer Hill Siding, 2 Sep 1995 (CNC); Mud Pond 1 km SE, 2 Sep 1995, (CNC); 1 km N Constance Lake, 2 Sep 1995 (CNC); Dwyer Hill Siding 3 km SE, 2 Sep 1995 (CNC); Prospect, Lanark 2 Sep 1995 (CNC). **QUEBEC:** Klock Rd., Aylmer, 2 Aug 1995 (CNC).

Observations of oviposition were made in the field by following females very slowly. Samples of plants upon which eggs were laid were identified using Semple and Heard (1987), and are deposited in the herbarium of Agriculture Canada in Ottawa (DAO). Larvae were reared

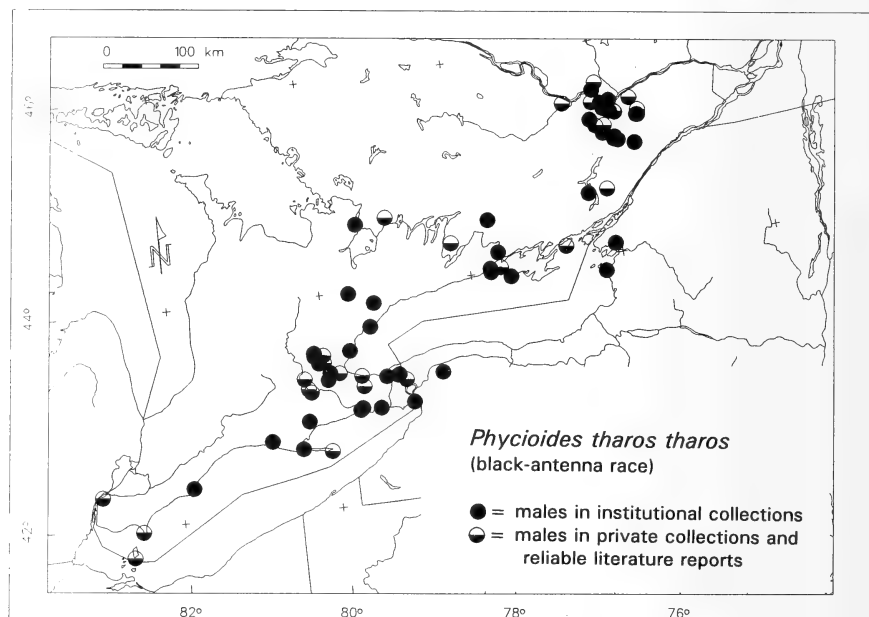


FIG. 1. Distribution of the black-antenna race of *Phycioides tharos tharos* in Ontario and adjacent regions. Based on males examined in institutional collections (dots, see Materials and Methods) and males in private collections or reliable literature reports of males (half-dots).

to adults on the same plants upon which the eggs were laid. Representative samples of butterflies were placed in CNC. Names for vascular plants listed for habitats were taken largely from Gleason and Cronquist (1991).

RESULTS AND DISCUSSION

Distribution. Oliver (1980) suggested that the region of sympatry of *P. tharos* and *P. cocyta* was equivalent to Remington's (1968) north-eastern suture zone and he noted a northern limit of *P. tharos* extending from central New England to southern New York, southern Ontario and southern Michigan. This northern limit, approximating the northern limit of the Carolinian or Upper Austral region of southern Ontario, was drawn by Scott (1986) and Opler & Malikul (1992) as extending from western Lake Ontario to southern Lake Huron. Figure 1 documents a northern limit extending farther north into the Canadian zone in the Ottawa valley north of Ottawa to 45°36'N (Lac Philippe) and to the southern edge of the Canadian Shield north of Lake Simcoe (Kirkfield and Orillia) at 44°38'N.

With extensive abandoned pasture and rich alvar habitats on the Bruce Peninsula and Manitoulin Island, one might expect *P. tharos* to

occur there, but these areas are cooler than the rest of the Ontario range. *Phyciodes tharos* was not represented among 43 *Phyciodes* males collected throughout this region at different times by J. A. Morton. It is also shown here for the first time in northern New York (Stony Point and Chaumont).

Currently *P. tharos* is known in Quebec only from the Ottawa valley (Eardley, Lac Phillippe, Aylmer). Of 125 *P. tharos* (*sensu lato*) at LEM, of which approximately half are males, there is only one with black antennal clubs (Laval, A. C. Sheppard, 19 Aug 1972), but the median and postmedian black lines on the upper wings are poorly developed, and the crescent patch is tan instead of dark brown. This specimen is consequently not clearly referable to *P. tharos*.

Various reports from Ontario (Hanks & Hess 1992, Hanks 1993, 1994, 1995) from localities north of those shown on Figure 1 were found to be referable to *P. tharos* in the earlier broad sense, and those that could be checked proved to be *P. cocyta* (the only exception being a report from Shoal Lake Road at Hwy 17 in Kenora district (Hanks 1994) that is not supported by a specimen; A. Wormington, pers. comm.). *Phyciodes tharos* occurs at similar latitudes in Manitoba (Klassen et al. 1989), Saskatchewan (Hooper 1973) and Alberta (Acorn 1993, Bird et al. 1995), and the western race with more yellow on the nudum quite possibly occurs in at least the southern Kenora and Rainy River portion of Ontario.

Status in Ontario. The relatively small number of *P. tharos* males in many institutional collections suggests the butterfly may be either rare in Ontario, or a recent arrival. The earliest collections of which I am aware are from St. Davids (43°10'N, 79°06'W) near the Niagara River in 1930 (UWO) and 1932 (CNC), and Brighton (44°02'N, 77°44'W) in Northumberland County in the eastern Lake Ontario region in 1932 (CNC). Even at this early date, Wild (1939) noted that some authorities considered the darker summer brood in the Niagara frontier region to be a distinct variety.

Although *P. tharos sensu stricto* may not be a recent arrival in the Lake Ontario region of Ontario, it was not noticed in the Ottawa valley until 1995, despite the fact that this region has received more attention from lepidopterists than any other part of Canada (Layberry et al. 1982). As soon as its habitats were understood it was found in at least 15 locations within the district (Crolla 1996); although it proved to be quite local, it is locally abundant and continuously present (the earliest collected specimen from the district was taken in 1990 at Eardley (F. Lessard, pers. comm.)). Some of the places from which it currently is known are at or near colonies of *P. batesii* which were visited a number of times by entomologists more than 65 years ago.

It seems unlikely that a few *P. tharos* would not have been taken by

the many early entomologists working in the region if it had been present, particularly in some of the habitats frequented by *P. batesii* at the time. Furthermore many of the current locations are abandoned pasturelands, which were part of a more intensively utilized agricultural landscape prior to 1960. Thus, it may have moved in over the past 30 years following abandonment of marginal pasturelands. Opler and Krizek (1984) speculated that *P. tharos* "probably expanded greatly with the cutting of eastern deciduous forests and expansion of agriculture."

On the other hand, *P. tharos* is quite local in the Ottawa valley and was previously lumped with *P. cocyta*, which is more conspicuous, widespread, and abundant early in the season. Consequently *P. tharos* may not have been collected "accidentally." Appropriate species-rich habitats undoubtedly existed within regional alvar landscapes (see Catling & Brownell 1995) in pre-settlement times due to fires, and it was collected as far north as Marmora in 1952.

Although *P. tharos* is clearly widespread in Ontario and occurs in both restricted natural habitats (alvars, dune slacks, prairies) and anthropogenic habitats (abandoned pastures and hay-old field complexes), the species does appear to be local and absent over vast areas. In contrast, its close relative *P. cocyta* is ubiquitous over much of the province in June and early July. *Phyciodes tharos* has been found in 65 locations and is currently known from at least 27 locations (where a location is defined as an area of occurrence at least 3 km from another area of occurrence). Consequently, its provincial ranking should be S3-S4, possibly uncommon but with sufficient occurrences to be secure, according to the Nature Conservancy of Canada system.

Oviposition and foodplants. In southern Quebec at Aylmer (45°14'N, 75°31'W) and in southern Ontario at Metcalfe (45°24'N, 53°75'W) and Dwyer Hill Siding (45°02'N, 75°49'W), females were observed ovipositing between 1300–1430 h. They flew short distances of 1–2 m, usually alighting and resting for 2–5 minutes, then crawled through the grasses and herbs 2–5 cm above the soil apparently searching for a foodplant. The crawls involved distances of 0.1–0.5 m and the crawling period lasted for 2–30 minutes with or without resting periods of up to 10 minutes (characterized by slow closing and opening of the wings to a horizontal position). During a crawl leading to oviposition a female moved over the same leaves 2–6 times with or without resting periods, and finally settled on the edge of a leaf with wings slowly closing and opening to an angle of 45°. The abdomen was curled under the leaf and pale green eggs were deposited adjacent to, or on top of others, on the lower leaf surface. The egg clusters included 52, 58 and 64 for the three locations listed above (respectively). Oviposition lasted approximately 20 minutes. The plant upon which eggs were laid at each of the three sites

was *Aster ciliolatus* Lindl. (Asteraceae), a species with elongate rhizomes that forms loose to dense patches. In all cases the females used relatively small, non-flowering rosette plants and placed eggs on leaves approximately 3 cm above the soil surface. The patches utilized were sparse rather than dense and lacked flowering plants, but the leaves upon which the eggs were laid were young and succulent. Larvae from the Aylmer site were reared on *Aster ciliolatus* from eggs to adult butterflies over 68–71 days (indoors).

Aster ciliolatus has not previously been reported as a foodplant of *P. tharos* (in either the broad or restricted sense). The range of this aster includes the boreal and mixed forest regions of eastern and central North America south to northern New England and the Great Lakes west across the northern edge of the prairie region (Semple & Heard 1987). Thus, this larval foodplant is only available at the northern range limit of *P. tharos*. It was present at all sites north of Lake Ontario and there was a clear correlation between the amount of it and the abundance of *P. tharos*. Further south in Ontario *Aster oolentangiensis* and *A. pilosus* are suspected larval hosts.

Habitats. The major habitat of the most northerly sites is dry, abandoned pasture with short grasses and rosette-forming herbs (e.g. *Danthonia spicata* and *Solidago nemoralis*), especially where these drier areas are interspersed with or adjacent to more moist open habitats. This habitat is prevalent in some alvar landscapes (i.e. areas supporting natural limestone barrens, see Catling and Brownell 1995) north of Lake Ontario. Here the abandoned pastures take a long time to develop complete tree and shrub cover because of the combined effects of moisture extremes, periodic drought and thin soil. Abundance of *Aster ciliolatus* and overall plant diversity is lower in the sites that have experienced the least past disturbance. Natural alvar complexes where tree and shrub cover is limited by fire or cutting, as well as drought, tend to have large populations of both *Aster ciliolatus* and *P. tharos* as well as a high diversity of both native and introduced plant species in a mosaic of wet and dry habitats. Landscapes where drought is the only factor have fewer plant associations, many of the potential open associations having developed tree or shrub cover.

Reduction in overall plant diversity due to reduction in kinds of open habitat in the less disturbed sites reduces nectar resources for adults: the less extreme site conditions associated with past or present reduction in woody cover allow flowering herbs to survive dry periods thus providing continuous resources for *P. tharos* adults. The continuity of nectar resources may be important to adult *P. tharos* since presence of the insect appears to be a consequence of continuous emergence (although there are definite peaks in some locations).

In the Burnt Lands alvar complex near Almonte, Ontario, fire was historically a factor in maintaining open conditions; but with a landscape broken by roads and quarries and with increasing development from housing, fires are no longer a significant environmental factor. In one extensive area, however, tree cover has been eliminated and shrub cover greatly reduced to improve the operation of radio towers, and this area contains a high plant diversity and *P. tharos* is locally abundant. The dominant plants in one of the major plant associations at this site include the grasses *Agrostis stolonifera*, *Carex pennsylvanica*, *Carex umbellata*, *Danthonia spicata* and *Poa pratensis*, and the herbs *Aster ciliolatus*, *Comandra umbellata*, *Fragaria virginiana*, *Prunella vulgaris*, *Senecio pauperculus*, *Solidago juncea*, *S. nemoralis*, and *S. ptarmicoides*.

The abandoned, rugged pastures on shallow, calcareous soil over limestone where *P. tharos* occurs are dominated by the grasses *Agrostis stolonifera*, *Danthonia spicata*, *Dactylis glomerata*, *Festuca* spp., *Poa compressa*, *Panicum philadelphicum*, *Sporobolus vaginiflorus*, and the herbs *Aster ciliolatus*, *Daucus carota*, *Echium vulgare*, *Fragaria virginiana*, *Hieracium pilloselloides*, *Leucanthemum vulgare*, *Melilotus alba*, *Origamum vulgare*, *Prunella vulgaris*, *Rudbeckia hirta*, *Senecio pauperculus*, *Solidago canadensis*, *S. nemoralis*, *Trifolium* spp. and *Vicia cracca*. The continuity of blossoms from spring through summer to fall in these habitats is to a large extent a result of the presence of introduced species. The nearly complete restriction of *P. tharos* to the dry alvar and abandoned limestone pasture habitats at its northern range limit could relate to the relatively warmer microclimate of these dry, open sites as well as to both adult and larval foodplant availability.

Farther south of the alvar landscapes and particularly in the Carolinian region of Ontario and northern New York, the main species of *Aster* associated with *P. tharos* at several sites is the white *A. pilosus*. Adult *P. tharos* occur in association with this species in natural habitats such as dune slacks dominated by the graminoids (grasses and sedges) *Cladium mariscoides*, *Poa compressa*, and *Schizachyrium scoparium*, and in old fields dominated by the grasses *Agrostis* spp., *Dactylis glomerata*, *Phleum pratense*, *Poa compressa*, *Poa pratensis*, and the herbs *Daucus carota*, *Solidago canadensis*, and *S. nemoralis*. Occupied habitats are primarily in areas of sandy soils subject to moisture extremes and where encroachment of shrubs such as *Cornus racemosa* is relatively prolonged. It also occupies hayfields that are cut once, but in these habitats there is probably an enforced displacement after cutting to adjacent uncut or abandoned fields. Cutting of hay results in a second or late blooming of *Daucus carota*, *Trifolium* spp., and other species, thus improving the local continuity of adult food resources. The hayfields often have *Trifolium* spp., *Lotus corniculatus*, *Dipsacus sylvestris*, *Ambrosia*

artemisiifolia among the dominants, the only prominent aster being *Aster pilosus* var. *pilosus*. In the dune slacks the prominent aster is usually *Aster pilosus* var. *pringlei*, but *A. dumosus* is also present.

In one prairie situation in southern Ontario (Brant County), *P. tharos* occurred in a hilly area dominated by *Schizachyrium scoparium*, *Sorghastrum nutans* and *Aster oolentangiensis* with no other *Aster* species evident. This site had been impacted previously by grazing and had many alien species. Other southern Ontario prairies surveyed were without populations of *P. tharos*.

In many cases *P. tharos* was found to be absent from areas within the general region of occurrence indicated in Figure 1. Some of the sand barrens and granite rock barrens searched had large populations of *Aster ciliolatus*, but there were periods of 4 weeks or more during the summer when nectar resources were essentially absent. In contrast, the closely related, and more or less univoltine, *P. cocyta* was present in most if not all of these sites. All sites where *P. tharos* was found including abandoned pastures, disturbed alvar, dune complexes, and hayfield-old field landscapes, had in common a high floristic diversity and a continuous supply of adult food resources, as a result of a mosaic of different habitats lacking woody cover.

Flight period. The earliest adult flight dates for Ontario are 22–26 May (Dunnville to the Ottawa district, respectively). The latest dates range from 13 October at Ottawa (pers. obs.) to 23 October on Point Pelee (Hanks & Hess 1992, reported by A. Wormington). Adult emergence appears to be almost continuous, with worn and fresh specimens of both males and females being found in most samples. At locations where there are large populations, adults were encountered from early June to early October. Appearance of the butterflies seems to depend as much on the weather as on a regular schedule of consecutive broods, but there were three clear peaks of abundance in 1995 (early June, mid-July to early August, and late August to early September).

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TWO NEW SPECIES OF ASTERACEAE-FEEDING *BUCCULATRIX* (BUCCULATRICIDAE) FROM CALIFORNIA

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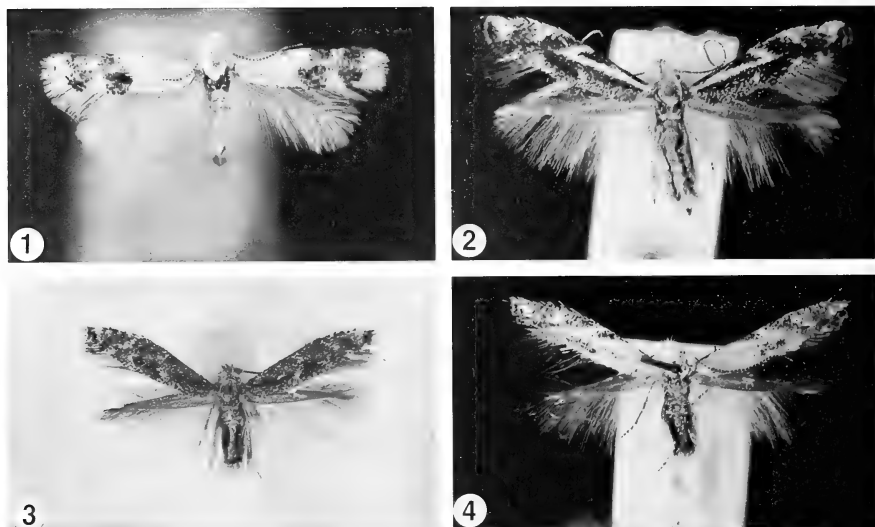
ABSTRACT. *Bucculatrix tetradyimiae*, new species and *Bucculatrix dominatrix*, new species are described and illustrated. *Bucculatrix tetradyimiae* feeds on *Tetradyimia axillaris* (Strother) (Asteraceae) and *Bucculatrix dominatrix* feeds on *Baccharis pilularis* (de Candolle) (Asteraceae) and can be distinguished from sympatric, *Baccharis*-feeding *Bucculatrix variabilis* (Braun) and *Bucculatrix separabilis* (Braun) by its larger size, distinct forewing pattern, and genitalia.

Additional key words: *Tetrydamia*, *Baccharis*, leaf miner, Lyonetiidae, microlepidoptera.

Zimmerman (1978) resurrected the family Bucculatricidae (Bucculatricidae) from Lyonetiidae, a move first proposed by Fracker (1915). The family is easily discerned, being characterized by an "elongate pointed face, tufted head, basal eye-cap of the antenna and, in the male, the notched first segment of the flagellum . . ." (Braun 1963). The larvae typically are leaf miners in the early instars, and then become external feeders, although a few species mature in the mine and some are gall-makers. For a complete description of the family refer to Braun (1963). The family is cosmopolitan with 222 species described from all land forms except New Zealand (Heppner 1991). More than 100 occur in North America, mostly in arid regions (Braun 1963). Larvae of many western species feed on Asteraceae, including the two species we describe here.

On 12 April 1993 in the western margin of the Mojave desert, California, we collected cocoons affixed to stems of the spiny shrub *Tetradyimia axillaris*. Cut branches with attached cocoons were immersed in buckets of water and transported to our homes in central California and so maintained. Adult *Bucculatrix* emerged during late April and early May.

David Wagner, John De Benedictis and Jerry Powell collected a new *Bucculatrix* on Mt. San Bruno (San Mateo Co.), where it is sympatric with the *Baccharis*-feeding *Bucculatrix variabilis* and *Bucculatrix separabilis*; De Benedictis et al. (1990:p.20) briefly described the adult cocoon and larval biology of this species without naming it. This species has also been reared from Marin County and Sonoma County by Jerry



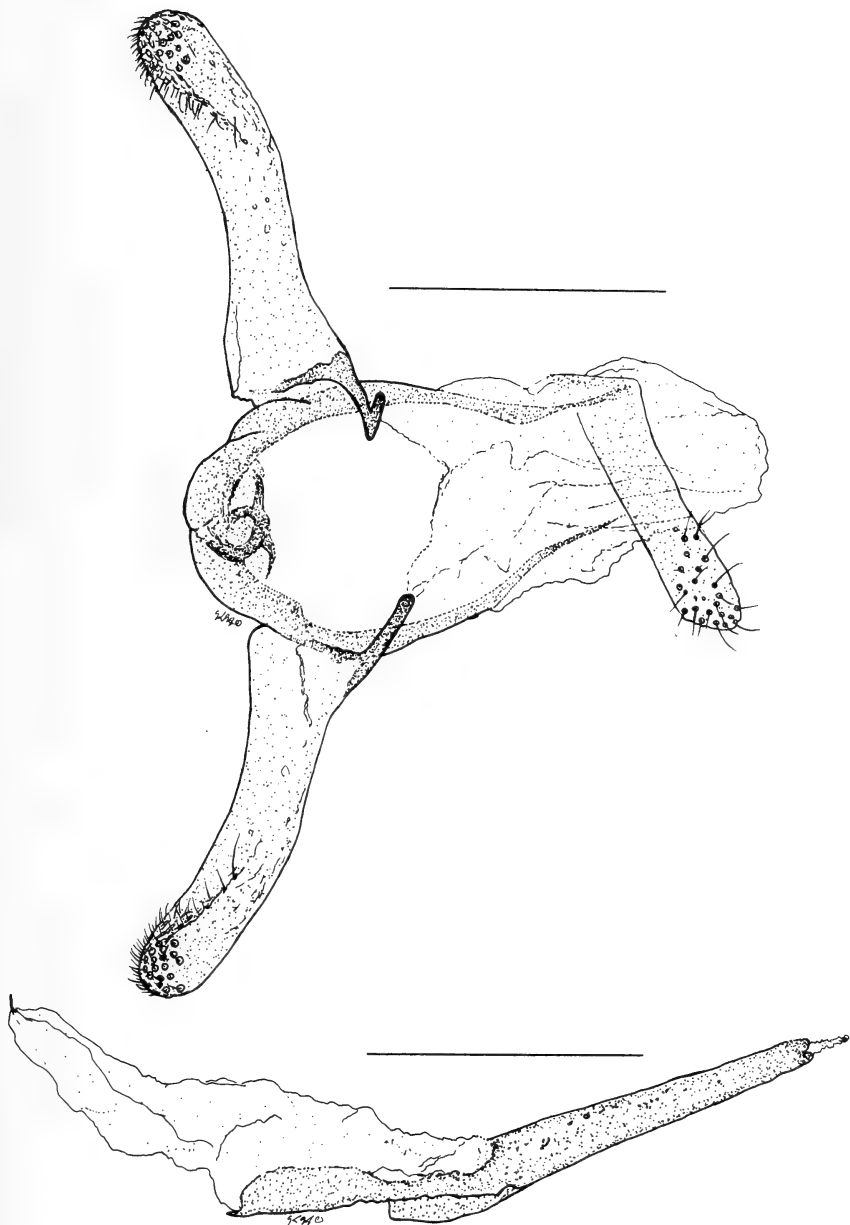
FIGS. 1–4. 1, *Bucculatrix tetradytmiae* paratype female. California: San Bernardino Co.: Oro Grande Wash, 5 mi. W. of Hesperia, 12 April 1993 (Rubinoff and Osborne), reared from cocoon on *Tetradytmia axillaris*, ex pupa 20 April 1993 (JAP 93D45). 2, *B. dominatrix* type female. California: Marin Co.: Ring Mountain, 19 April 1991 (J. A. Powell), reared from cocoon on *Baccharis pilularis*, ex pupa 1–2 May 1991 (JAP 91D16). 3, *Bucculatrix variabilis*. California: Monterey Co. Big Creek Reserve (UCNRS), 1–3 May 1992 (J. A. Powell) reared from cocoon on *Baccharis pilularis*, ex pupa 6 May 1992 (JAP 92E11). 4, *Bucculatrix separabilis*. California: Napa Co. 1 mile SE of Angwin, 20 May 1980 (J. A. Powell).

Powell and David Wagner, respectively. Both new species were sexed on the basis of frenulum morphology and external genitalia.

Bucculatrix tetradytmiae Osborne and Rubinoff, new species (Figs. 1, 5–8)

Description. *Head.* White; antenna white with white basal eye-cap and dark brown annulations. *Thorax.* White. *Forewing.* Length: mean 3.4mm (range 3.2–3.8mm, $n = 29$). Dorsal surface lustrous white with distal half dominated by roughly equal-sized postmedial and submarginal blotches partially separated by white at anal angle and costa. Blotches, ochreous brown, tipped with dark brown. Postmedial blotch often bisected by diffuse longitudinal white or light brown. Occasionally blotches greatly reduced. Below fold, in proximal extreme of postmedial blotch, a very dark patch of completely and partially dark brown scales. Series of white, dark-tipped scales running dorsally from apex along margin to merge with distal edge of dark field. Usually a small patch of several dark brown tipped scales on costa at 1/3 from base to apex. Cilia brown above brown field on costa, white subapically, brown in streak at apex on apical end of marginal chain of brown scales, all white along margin. Ventral surface of forewing gray-brown. *Hindwing.* Gray dorsally, gray-brown ventrally with gray cilia. *Leg.* White with dark brown annulations on distal ends of tarsal segments. Metathoracic tibiae with long white cilia. *Abdomen.* Gray. Terminal scales elongate and dark gray dorsally in females.

Male genitalia (Figs. 5, 6 drawn from YFH prep no. 0911). Valva elongate, slightly curved medially with fine distal setation. Socii divergent, elongate, with long setae on dis-



FIGS. 5, 6. 5, *B. tetradymiae* paratype male genitalia. 6, aedeagus of same. Slide YFH 0911. California: San Bernardino Co., Oro Grande Wash, 5 mi. W. of Hesperia, 25 April 1993 (D. Rubinoff). Scale bars = 1 mm.

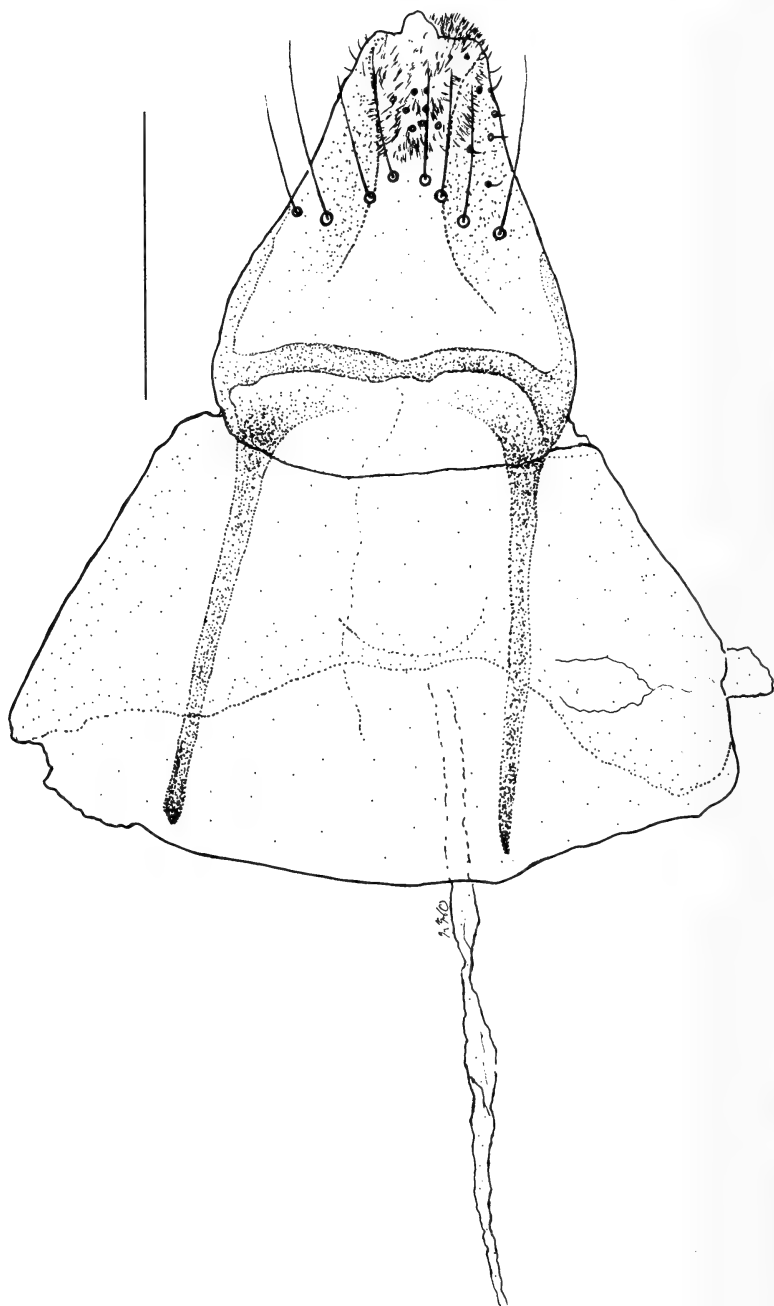


FIG. 7. *B. tetradymiae* paratype female genitalia. Slide YFH 0905. California: San Bernardino Co., Oro Grande Wash, 5 mi. W. of Hesperia, 25 April 1993 (D. Rubinoff). Scale bars = 1 mm.

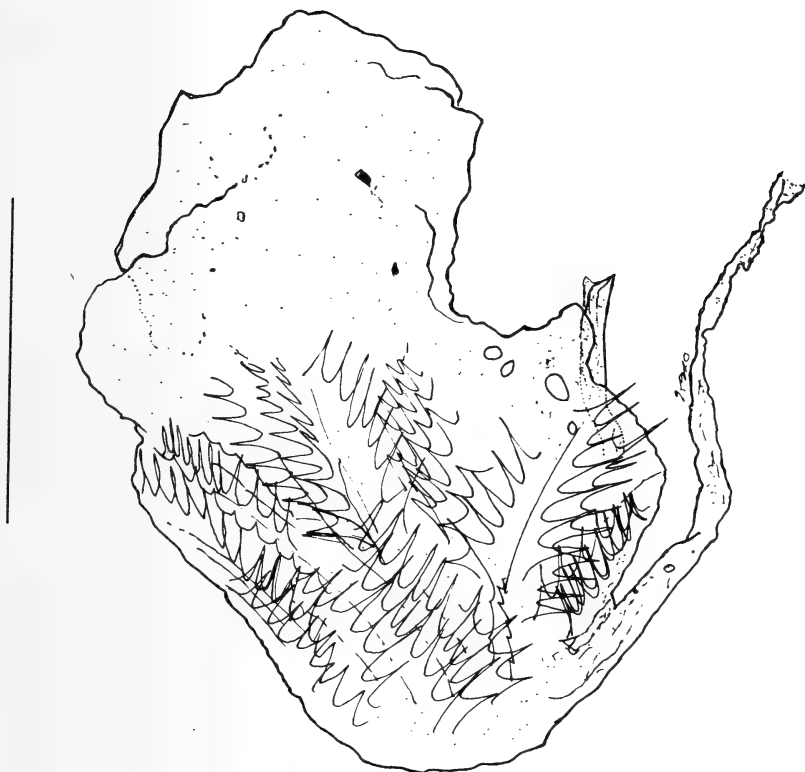


FIG. 8. *B. tetradymiae* paratype female genitalia, corpus bursae. Slide YFH 0906. California: San Bernardino Co., Oro Grande Wash, 5 mi. W. of Hesperia, 25 April 1993 (D. Rubinoff). Scale bars = 1 mm.

tal third. Gnathos absent. Vinculum narrow, well sclerotized. Aedeagus straight, gradually tapering to slender apex.

Female genitalia (Fig. 7 drawn from YFH prep no. 0905, Fig. 8 drawn from YFH prep no. 0906). Ductus bursae not sclerotized. Margins of ostium bursae weakly sclerotized. Ostium in anterior margin of abdominal segment eight. Ninth tergum with transverse row of long, stout setae at mid-segment. Posterior apophyses about length of abdominal segment eight, well sclerotized. Anterior apophyses absent. Ductus seminalis arising on corpus bursae near base of ductus bursae. Signum strong, nearly encircling posterior half of bursa, ribbed with long aciculae; converging toward base of ductus bursae.

Type specimens. *Holotype* ♂, California: San Bernardino Co.: Oro Grande Wash, 5 mi. W. of Hesperia, 12 April 1993 (Rubinoff and Osborne), reared from cocoon on *Tetradymia axillaris*, ex pupa 20 April 1993. *Paratypes* (n = 49): California: San Bernardino Co.: Oro Grande Wash, 5 mi. W. of Hesperia, 1 ♂, 1 ♀, 12 April 1993 (Rubinoff and Osborne), reared from cocoons on *Tetradymia axillaris*, ex pupa 20 April 1993; also 2 ♂, 6 ♀, 25 April 1993 (Rubinoff and Osborne) reared from cocoons on *Tetradymia axillaris*, ex pupa 1–3 May 1993 (JAP 93D48); also 17 ♂, 1 ♀, 27 April 1996 (Osborne); also 18 ♂, 3 ♀, 29 April 1996 (Osborne). The holotype and 26 paratypes are deposited at the Essig Museum of Entomology, University of California, Berkeley (UCB); 4 paratypes are deposited in the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.

(USNM); 4 paratypes are deposited in the University of Connecticut collection at Storrs (UCONN); 3 paratypes are deposited in the Los Angeles County Museum (LACM); 3 paratypes are deposited in the Canadian National Collection of Insects (CNCI); 3 paratypes are deposited in the California Academy of Sciences (CASC); 4 paratypes remain in the collection of Kendall Osborne and 2 paratypes in the collection of Daniel Rubinoff.

Diagnosis and discussion. *Bucculatrix tetrydamiae* is a small, white bucculatricid with brown blotches dominating the outer half of the forewing. *B. tetrydamiae* keys out to *Bucculatrix packardella* (Chambers) (of the eastern United States) in Braun's (1963) key to the adults based on maculation. The oak-feeding *B. packardella* differs from *B. tetrydamiae* by the brown speckles over the face, eye-caps and thorax, and by the dusting of brown-tipped scales over the forewing base. On the basis of genitalic characters and host specialization, *B. tetrydamiae* falls within Braun's (1963) section II of *Bucculatrix* which contains the majority of North American, Asteraceae-feeding *Bucculatrix*; *B. packardella* is assigned to section IV.

Adult moths are found in close association with the host, *Tetradymia axillaris*, in the western Mojave Desert. The early stages probably mine the glabrose, fascicular leaves while the late stage larvae feed externally. The white cocoons were fixed lengthwise usually against axillary spines of the host, are mostly smooth with slight ridges discernible on the caudal terminus. This unusual smoothness (most *Bucculatrix* cocoons have conspicuous sculpturing) is not due to the cocoon-smoothing effects of parasitoids, as hypothesized by Braun (1963) since many of our cocoons were viable. Adults emerged between 20 April and 10 May 1994 in captivity from cocoons kept both indoors (room temperature) and outdoors in Berkeley, California.

We saw many adults on *Tetradymia* at Oro Grande Wash on 23 April 1994, but we found none when we returned on 13 May 1994. Adults are active from at least 1600 to 2000 hours. Females extrude the papillae anales while resting on the host plant and males rapidly crawl (about 1 cm per second) along the length of stems usually searching each axillary spine in sequence along a stem, then crawling or sometimes flying to a new stem. An observed mating lasted 45 minutes. All known specimens come from the type locality although the species should be expected over much of the Mojave desert and may extend over the range of its host.

***Bucculatrix dominatrix* Rubinoff and Osborne, new species**

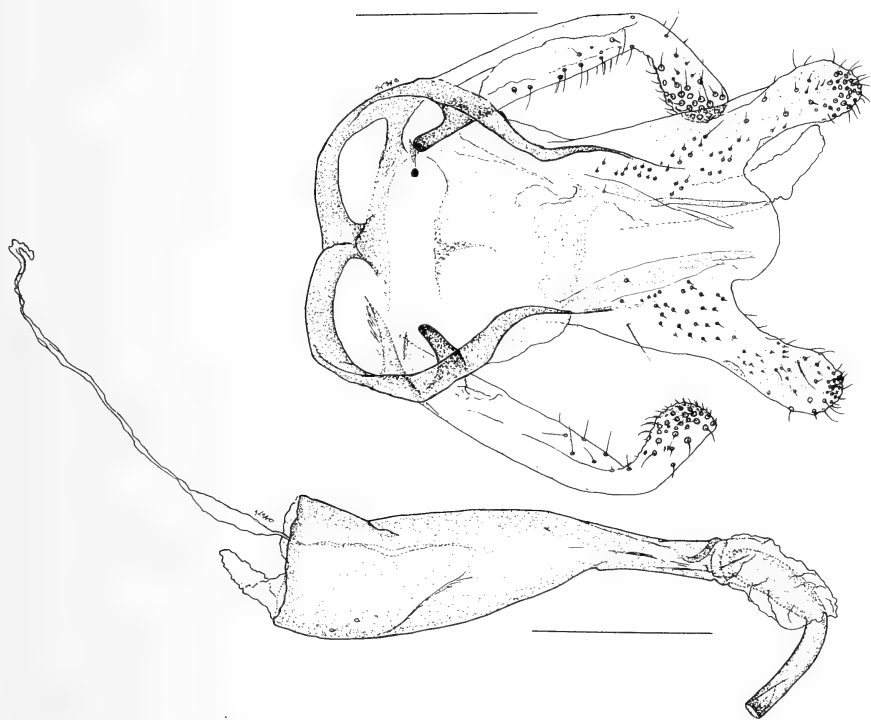
(Figs. 2, 9–12)

Description. *Head.* Grayish white, tuft brown and white hairs, eye-caps gray; antenna black and white banded. *Thorax.* grayish-white with scattered brown-tipped scales. *Forewing.* Length: mean: 5.5 mm (range: 4.0–6.1mm, n = 32), mottled brown, prominent longitudinal white streak extending above Cu from base along the discal cell, then abruptly jutting at acute angle towards costal margin. Just below Cu at acute angle in white streak, small, very dark patch of scales, just below (fold) vein. Distally, mottling becoming lighter, ending nearly white and surrounded by fuscous-tipped apical scales. Cilia gray. Ventral surface iridescent brown. *Hindwing.* Pale gray, ventral surface iridescent brown. *Leg.* Gray with distal end of tibia turning black. Tarsi banded with black and white. *Abdomen.* Silvery gray.

Male genitalia (Figs. 9, 10 drawn from YFH prep no. 0903). Valva elongate, pointing inwards at the setose distal ends. Soci divergent, very broad, more setose apically, and fused with tegumen. Saccus absent. Vinculum well-sclerotized band. Uncus poorly sclerotized with distal end obtuse. Aedeagus arising from tapered annellus. Distinguished from male genitalia of *B. variabilis* by much shorter, stout socii; very similar to male genitalia of *B. separabilis*.

Female genitalia (Figs. 11, 12 drawn from YFH prep no. 0907). Ostium in deep, well-sclerotized, cup-shaped chamber. Corpus bursae ovoid. Ductus seminalis originating on corpus bursae just dorsal to junction of ductus bursae and corpus bursae, no expansion of ductus seminalis apparent. Signum narrow, forming densely spined band of ribs at the posterior end of corpus bursae just anterior of where ductus seminalis and ductus bursae join corpus bursae.

Type specimens. *Holotype* ♀, California: Marin Co.: Ring Mountain, 19 April 1991



FIGS. 9, 10. **9**, Paratype male genitalia of *B. dominatrix*. **10**, aedeagus of same. Slide YFH 0903. California: Marin Co., Ring Mt., 19 April 1991 (J. A. Powell) reared from cocoon on *Baccharis pilularis*, ex pupa 1–5 May 1991 (JAP 91D16). Scale bars = 1 mm.

(J. A. Powell), reared from cocoon on *Baccharis pilularis*, ex pupa 1–2 May 1991 (JAP 91D16). *Paratypes* ($n = 42$): California: Marin Co.: Ring Mountain, 6 ♂, 5 ♀, 11 April 1994 (J. A. Powell), reared from cocoons on *Baccharis pilularis*, ex pupa 20–26 April 1994 (JAP 94D53); also, 6 ♂, 2 ♀ 19 April 1991 (J. A. Powell), reared from cocoons on *Baccharis pilularis*, ex pupa 1–5 May 1991 (JAP 91D16); San Mateo Co.: Mt. San Bruno County Park, 3 ♂, 2 ♀, 19 April 1988 (J. A. DeBenedictis) at b.l., also 3 ♂, 4 ♀, 21 April 1983 (J. A. DeBenedictis), reared from cocoons on *Baccharis pilularis*, ex pupa 11–17 May 1983 (JADeB 83111-E), also 1 ♀, 14 April 1983 (J. B. Whitfield), reared from cocoon on *Baccharis pilularis*, ex pupa 3 May 1983 (JAP 83D70); Alameda Co.: Strawberry Canyon, UCB campus, 1 ♂, b.l. trap, 1 July 1991 (J. A. Powell), also 1 ♂, 20 June 1990 (J. A. Powell); Sonoma Co.: 1 mi. SE Bodega Bay, 4 ♂, 4 ♀, 20 April 1983 (D. L. Wagner), reared from cocoons on *Baccharis pilularis*, ex pupa 3–24 May 1983 (JAP 83D110). The holotype and 20 paratypes are deposited in the Essig Museum of Entomology at the University of California, Berkeley (UCB); 3 paratypes are deposited in the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); 11 paratypes are deposited in the University of Connecticut collection at Storrs (UCONN); 2 paratypes are deposited in the Canadian National Collection of Insects (CNCI); 2 paratypes are deposited in the Los Angeles County Museum (LACM); 2 paratypes are deposited in the California Academy of Sciences (CASC); 1 paratype remains in the collection of Kendall Osborne and 1 paratype in the collection of Daniel Rubinoff.

Diagnosis and discussion. *Bucculatrix dominatrix* is relatively large and distinguishable by a prominent white streak on the upper part of the discal cell, extending two-

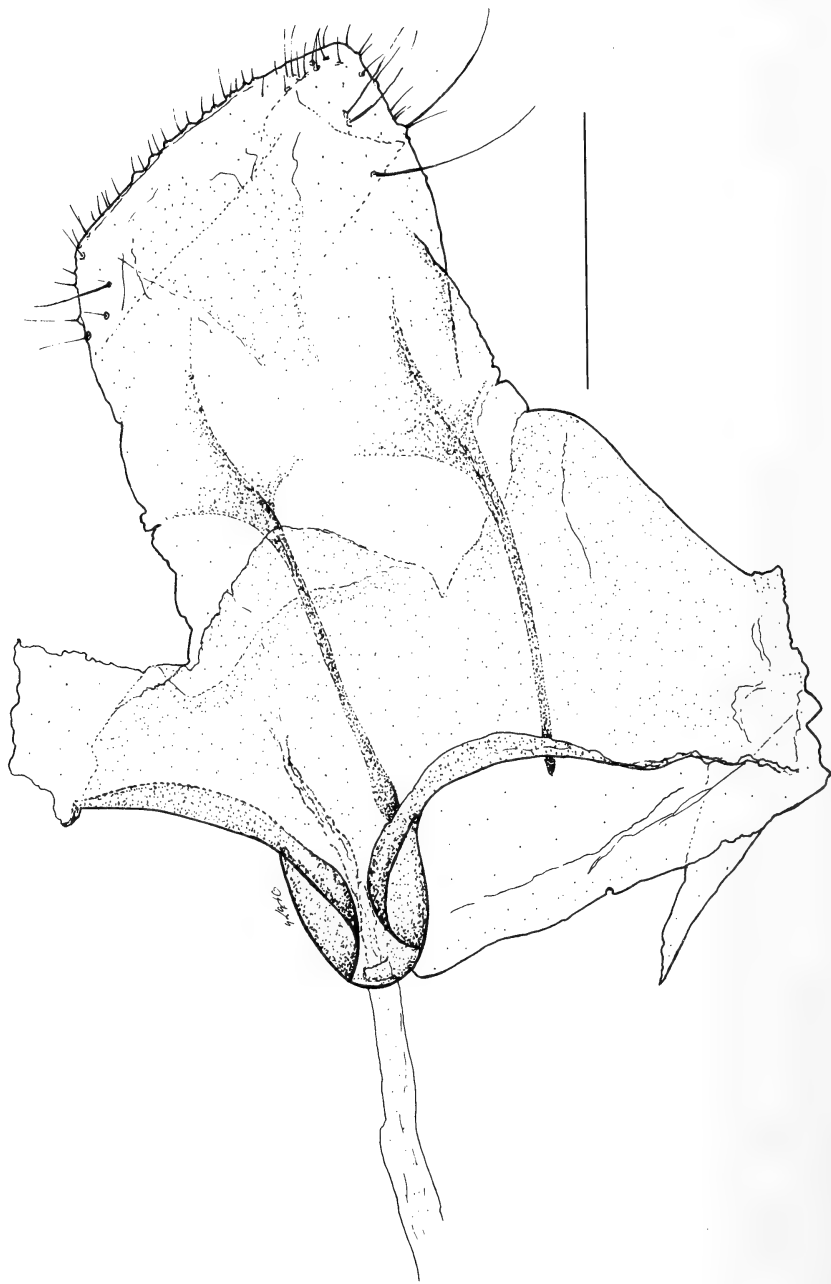


FIG. 11. Paratype female genitalia of *B. dominatrix*. Slide YFH 0907. California: Marin Co. Ring Mt., 19 April 1991 (J. A. Powell) reared from cocoon on *Baccharis pilularis*, ex pupa 1–5 May 1991 (JAP 91D16). Scale bars = 1 mm.

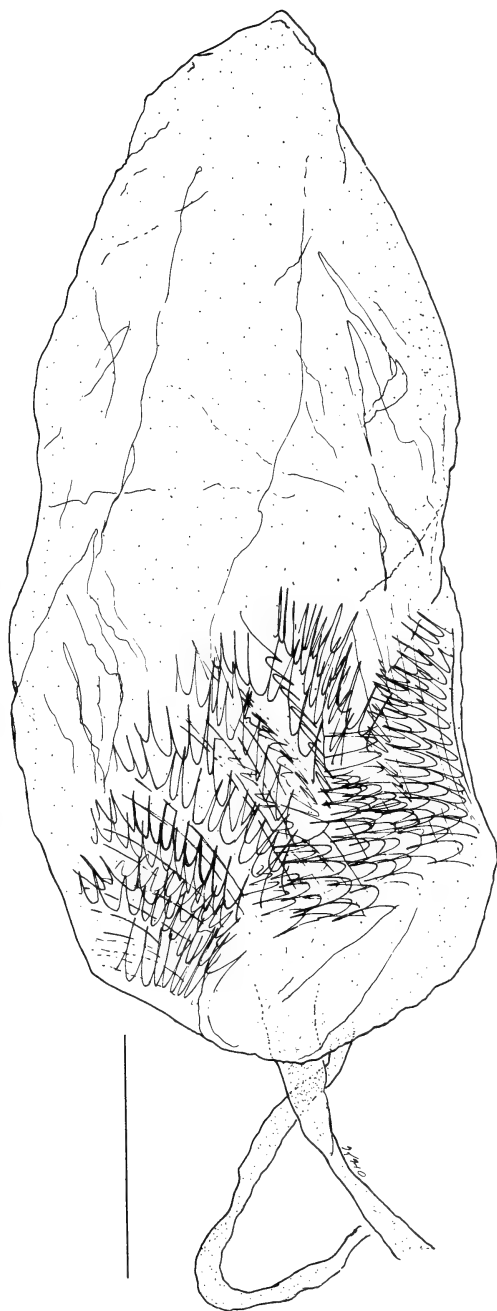


FIG. 12. Paratype female genitalia of *B. dominatrix*, bursa copulatrix. Slide YFH 0907. California: Marin Co. Ring Mt., 19 April 1991 (J. A. Powell) reared from cocoon on *Baccharis pilularis*, ex pupa 1–5 May 1991 (JAP 91D16). Scale bars = 1 mm.

thirds the length of the wing. *B. dominatrix* is probably a close relative of both *Bucculatrix variabilis* (Fig. 3) and *B. separabilis* (Fig. 4) and phenotypically resembles the former. The new species is 1.5 to 2 times larger than *B. variabilis*. The forewing pattern is diagnostic: *B. variabilis* has two transverse white bands whereas *B. dominatrix* has a single, longitudinal white streak. There is also a tuft of dark scales below the longitudinal band that is not present in *B. variabilis*. *B. dominatrix* is larger and much darker than *B. separabilis* but the genitalia are nearly identical, indicating a probable sister species relationship between the taxa. Phenotypic and genitalic similarities to the two aforementioned species merit its placement in Section II, subsection A, of Braun (1963). Average cocoon length is 8.1 mm (range: 6.5–11.5 mm, $n = 20$). They are strongly ribbed and pinkish when occupied (DeBenedictis et al. 1990) turning white after emergence.

Bucculatrix dominatrix may be widely distributed in coastal central California, where the hostplant is found. It feeds on *Baccharis pilularis* and can be found feeding on the same plants as both *Bucculatrix variabilis* and *B. separabilis*.

ACKNOWLEDGMENTS

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A REVISION OF THE *CERASTIS CORNUTA* GROUP OF THE GENUS *CERASTIS* SUBGENUS *METALEPSIS* (NOCTUIDAE)

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ABSTRACT. The noctuid genera *Cerastis* Ochseneimer and *Metalepsis* Grote are reviewed resulting in revision of *Metalepsis* to a subgenus of *Cerastis*. The *C. cornuta* group of *Cerastis* subgenus *Metalepsis* is defined. In addition to *cornuta* Grote, this group contains three new species: *C. enigmatica*, new species from the Pacific Northwest; *C. robertsoni*, new species from southern California; and *C. gloriosa*, new species from the west coast of the continental United States. The species are illustrated and a key for their identification is presented.

Additional key words: California; Pacific Northwest; sphagnum bog; coastal chaparral.

Cerastis Ochseneimer is a genus of 13 species of medium-sized moths which occur in temperate forests of the Holarctic region. They are unusual in the subfamily Noctuidae in that the adults are active in early spring, flying with species in the subfamilies Psaphidinae, Hadeninae and some Ipimorphinae (Xylenini: *Lithophane*, *Eupsilia*).

The North American species of *Cerastis* were previously arranged in two genera. Three species with foretibial spines constituted *Metalepsis* Grote. The type species of *Metalepsis*, *cornuta* Grote, 1874, occurs on the west coast and was thought to have a range extending north from its type locality, California, to the Alaska Panhandle. A new species allied to *C. cornuta* was recently discovered on the coast of California and Washington. Subsequent study of the populations previously considered to be *C. cornuta* revealed that these consisted of three allopatric species. *Cerastis cornuta* is restricted to central California and populations to the north and south of its range, although superficially similar, are distinct species differentiated by genitalic characters.

The relationship of *Metalepsis* to *Cerastis* was re-evaluated as part of our study of the *C. cornuta* group. McDunnough (1927), recognizing the close relationship of these genera, stated that "the male genitalia of the two genotypes are practically identical." He retained *Metalepsis* for the species with sclerotized setae ("spines") on the tibia of the prothoracic leg. This treatment was followed in subsequent checklists and cat-

alogs of North American noctuid moths (McDunnough 1938, Franclemont & Todd 1983, Poole 1989).

We retain *Metalepsis* as a subgenus, **new status**, of *Cerastis*. These two subgenera are distinguished by the shape of the digitus, the presence or absence of sclerotized foretibial setae, and the shape of segment A8 in the female. In subgenus *Cerastis* the digitus is immediately distal to the clasper and is free from the inner surface of the valve for most of its length, the foretibiae are devoid of setae, and abdominal segment eight of the female forms lobes which project into each side of the ostium bursae. In subgenus *Metalepsis* the digitus is fused to the inner surface of the valve for most of its length with only the apical third to quarter free, the tibia of the first leg bears complete inner and partial outer rows of sclerotized setae, and the ostium bursae is without lobes. There are seven species in subgenus *Cerastis*, *tenebrifera* (Walker 1865) in North America and six in Eurasia (Fibiger 1993). The six species in subgenus *Metalepsis* are restricted to North America. The revised status of *Metalepsis* results in the following new combinations for these species: *Cerastis cornuta*, **new combination**; *Cerastis fishii*, **new combination**; and *Cerastis salicarum* (Walker 1857), **new combination**.

The species in these subgenera share derived characters of adults and larvae indicating that they form a monophyletic group and should be united in one genus: male antennae bipectinate (reduced in *C. fishii* (Grote 1878) and the Old World *C. rubricosa* [Denis and Schiffermüller] 1775); head and thorax covered with hairlike scales; male genitalia with anellus sclerotized laterally and covered with short stout spines, valve with digitus but lacking a corona, and vesica coiled in a single loop with one or more large basal cornuti; female genitalia with bisaccate bursa and membranous ventral cleft in the sclerotization of the ductus bursae; larva with ridges on inner surface of mandible extending to the cutting margin without a tooth on the inner surface, and with stemmata 3 and 4 very close together, almost touching.

The presence of the digitus is unusual in the subfamily Noctuidae and is probably a primitive condition. *Choephora* Grote, type species *Choephora fungorum* Grote & Robinson, 1868, is the genus most closely related to *Cerastis*. The two genera share the distinctive characters of the anellus and larvae and the antennae, vestiture and shape of the valves are similar. *Choephora* differs from *Cerastis* in lacking the digitus on the valve and in its mid-summer flight season.

The *Cerastis cornuta* group includes four species, three of which are described as new. All four are restricted to the west coast of North America. The adults are easily distinguished from other species in the subgenus by the distinctive forewing spots which are conspicuously outlined with pale scales. The elongate oblique orbicular and reniform

spots are fused across the median space in most specimens, forming a broad V. The uncus of the male genitalia is broadest apically in the *C. cornuta* group but subapically in other *Cerastis*. The four species are superficially similar and can most reliably be distinguished by genitalic characters, however, subtle differences in wing pattern and length can be used to separate some specimens without dissection. Identification is simplified since only *Cerastis gloriosa* occurs sympatrically with other species in the group. *Cerastis gloriosa* is the most distinctive species and can usually be identified without dissection, allowing the three remaining species to be tentatively identified by geographic location.

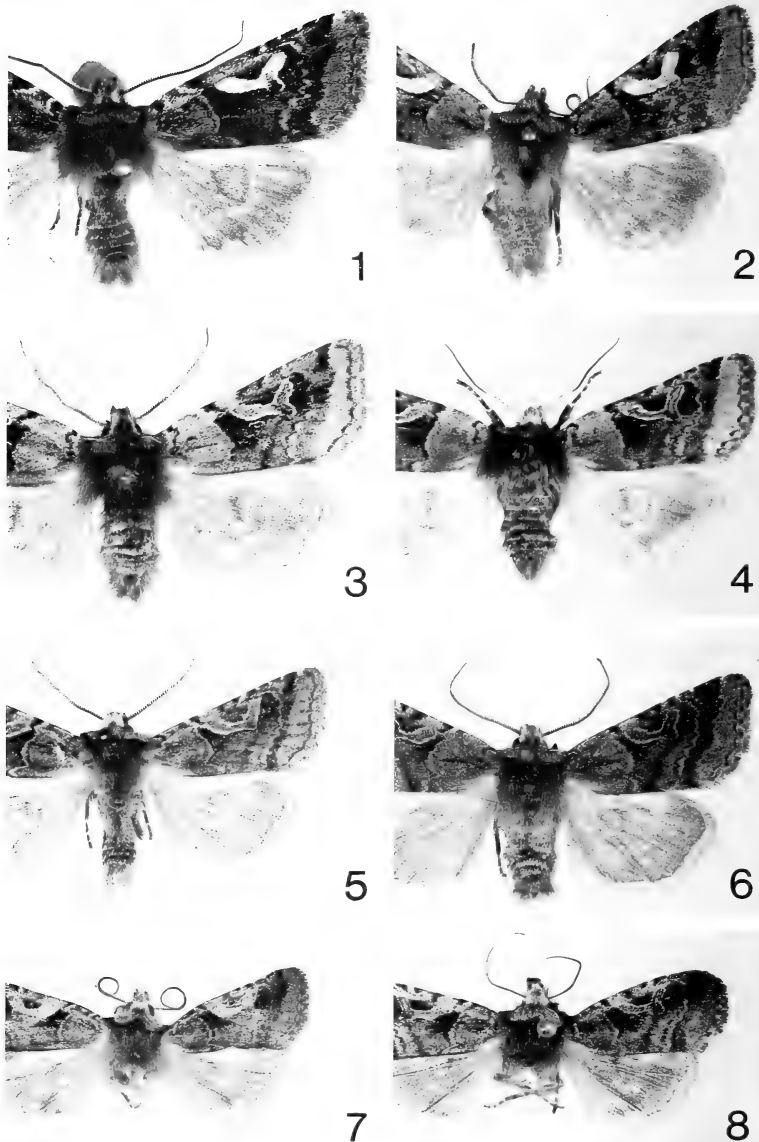
The terminology for wing pattern and genitalia structures follows that used in the *Moths of America North of Mexico* series. These are illustrated by Hodges (1971: vi–vii).

Key to adults of the *cornuta* group of *Cerastis*

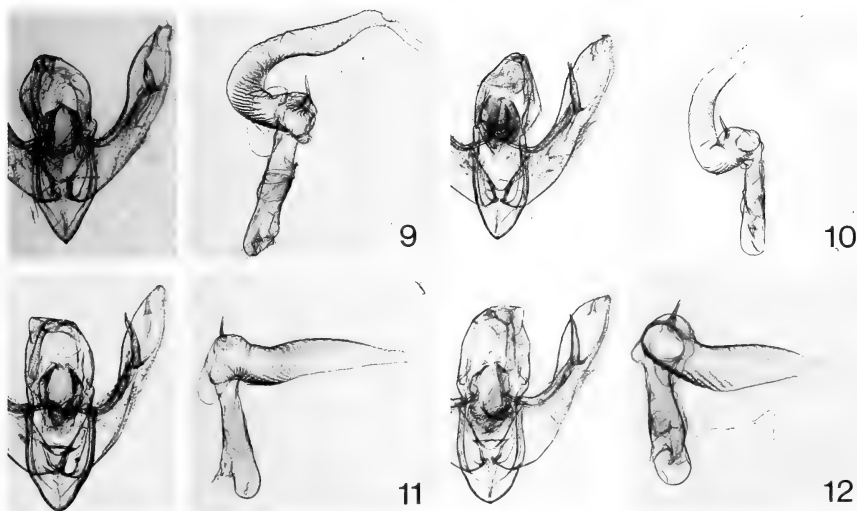
- 1. Orbicular spot mostly filled with white or pale yellow (Figs. 1–2); larger species, forewing length 14–17 mm; male antenna 2× as wide as the central shaft; clasper short, projecting posteriorly, not reaching dorsal margin of valve (Fig. 9); appendix bursae smaller than corpus bursae with ductus seminalis at posterior end (Fig. 13) *C. gloriosa*
- 1'. Orbicular spot gray or brown, usually outlined in yellow (Figs. 3–8); smaller species, forewing length 11–15 mm; male antenna 3× as wide as central shaft; clasper extending posterodorsally beyond dorsal margin of valve (Figs. 10–12); appendix bursae larger than corpus bursae with ductus seminalis at anterior end (Figs. 14–16) 2
- 2. Vesica with a basal coil, bent ventrad 90° near base then to left, curving in an arc over 180° to project posterolaterally to the right (Fig. 10); appendix bursae joined to corpus bursae 1/3 from posterior end and extending obliquely towards corpus bursae anteriorly (Fig. 14); occurring in Cascades and West Coast from the Alaska Panhandle to northern California (Humboldt County) *C. enigmatica*
- 2'. Vesica bent 90° once or twice at base, then nearly straight (Figs. 11–12); appendix bursae joined to corpus bursae at posterior end and extending obliquely away from corpus bursae anteriorly (Figs. 15–16); occurring in western California 3
- 3. Vesica bending 90° ventrad near base, then straight (Fig. 11); appendix bursae even in width from base to apex, nearly straight, projecting slightly anteriorly at apex (Fig. 15); ductus bursae shorter, 1.5× as long as wide; occurring along the coast from San Francisco Bay to Sonoma County *C. cornuta*
- 3'. Vesica with two 90° bends near base, bending ventrad for distance equal to aedaeagus width and then laterally to left (Fig. 12); appendix bursae constricted apically, curving dorsally at apex (Fig. 16); ductus bursae 2× as long as wide; occurring in Coast Range from Monterey Bay to Santa Barbara County *C. robertsoni*

Cerastis gloriosa Crabo & Lafontaine, new species
(Figs. 1, 2, 9, 13)

Description. *Male* (Figs. 1, 2): *Head*: dark reddish brown; palpi concolorous. *Eyes*: black. *Antennae*: bipectinate, 2x as wide as central shaft. *Thorax*: dark reddish brown; collar lighter, reddish brown with darker lines. *Foretibiae*: spined. *Forewing*: length 14–17 mm; dark reddish brown, suffused with variable amounts of black in discal cell; basal area with gray scales and violaceous tint; terminal area lighter than remainder of forewing, also with violaceous tint; lines double, black, pale filled; basal line sinuous; antemedial line oblique, gently excurved, notched sharply basad in fold; median shade usually obsolete, when present weak, wavy, evident only from reniform spot to inner margin; postmedial



FIGS. 1-8. Adults of *Cerastis* spp. 1, *C. gloriosa* Crabo & Laf., paratype ♂, North Bay Bog, Grays Harbor County, Washington; 2, *C. gloriosa* Crabo & Laf., ♂, Mill Valley, California; 3, *C. enigmatica* Laf. & Crabo, holotype ♂, Vancouver, British Columbia; 4, *C. enigmatica* Laf. & Crabo, paratype ♀, Wellington, British Columbia; 5, *C. cornuta* (Grote), ♂, Inverness, Marin County, California; 6, *C. cornuta* (Grote), ♂, Bodega, Sonoma County, California; 7, *C. robertsoni* Laf. & Crabo, paratype ♂, Gaviota Pass, Santa Barbara County, California; 8, *C. robertsoni* Laf. & Crabo, paratype ♀, Gaviota Pass, Santa Barbara County, California.



FIGS. 9–12. Male genitalia of *Cerastis* spp. **9**, *C. gloriosa* Crabo & Laf., Mill Valley, California, CNC 10296; **10**, *C. enigmatica* Laf. & Crabo, Ketchikan, Alaska, CNC 11140; **11**, *C. cornuta* (Grt.), Oakland, California, CNC 11139; **12**, *C. robertsoni* Laf. & Crabo, Gaviota Pass, Santa Barbara County, California, CNC 11135.

line dentate, lower half nearly straight, excurved opposite cell; subterminal line weak, pale, undulating, with strong wedge-shaped black patches proximally opposite discal cell between median veins and near costa on radial veins; terminal line thin, weakly scalloped; claviform spot narrow, black; orbicular spot large, an elongate ellipse, usually broadly fused with reniform spot; reniform spot large, it and orbicular spot yellow gray, partially to almost completely filled with and outlined by white or light yellow scales. *Hindwing*: medium to dark fuscous with red tint; with faint median shade and discal lunule. *Abdomen*: light gray to reddish brown. *Female*: similar to male.

Male genitalia (Fig. 9). Uncus cylindrical at base, broadest at apex; with hairlike setae. Anellus heavily sclerotized laterally, covered apically with short stout spines. Juxta triangular with short dorsomedian extension. Valve 6× as long as wide, constricted near middle; apex of valve drawn to a blunt point, without corona; sacculus 1/2 as long as valve and extending to dorsal margin of valve; clavus absent; ampulla of clasper gently curved, extending posteriorly without reaching dorsal margin of valve; basal 2/3 of digitus fused to valve, distal 1/3 free, finger-like. Vesica approximately 1.5× as long as aedeagus, with simple and large bilobed subbasal diverticula; single subbasal cornutus, slightly longer than aedeagus width, gently curved; distal 2/3 of vesica U-shaped; vesica projecting ventrally at base, then bending through 180° arc to project dorsally.

Female genitalia (Fig. 13). Corpus bursae ovoid, lacking signa. Appendix bursae arising from posterior end of corpus bursae on right, shorter than corpus bursae, broad, slightly U-shaped posteriorly (apparently curving back on itself) with ductus seminalis at posterior end. Ductus bursae broad, dorsoventrally flattened, heavily sclerotized, sclerotization of ventral wall split by membranous cleft, ventral wall of ductus bursae produced ventrad into a small pouch at junction with corpus bursae. Anterior apophysis 1/4 length of posterior apophysis. Ovipositor lobes triangular, covered with short and long setae.

Type specimens. *Holotype*: ♂; WASHINGTON: Grays Harbor Co.: North Bay Bog, 0.6 mi N of the North Bay of Grays Harbor, 47.05°N 124.09°W, elev. 5 m, 12 IV 1991, leg. L. G. Crabo, Native cranberry bog. *Paratypes*: 52 ♂; OREGON: Clatsop Co.: Coastal Plain, Ocean Home Farm 1.3 mi N of Gearhart, 46.04°N 123.90°W, Elev. 25', 24 III 1993,

L. & A. Crabo leg., bog E of last inland dunes (1 ♂). WASHINGTON: Type locality: 30 III 1991, L. G. Crabo (5 ♂), 12 IV 1991, L. G. Crabo (16 ♂), 26 III 1993, J. Troubridge (1 ♂), 1 IV 1994, J. & L. Troubridge (15 ♂); Grays Harbor Co.: 0.6 mi NW of Carlisle on Ocean Beach Rd., 47.16°N 124.10°W, elev. 20 m, 15 IV 1990, L. G. Crabo, native cranberry bog (15 ♂). The holotype is in the Canadian National Collection (Ottawa). Paratypes are in the Canadian National Collection (Ottawa), University of California (Berkeley), University of California (Davis), Oregon State University (Corvallis), and the personal collections of Lars Crabo (Bellingham, Washington), Ron Robertson (Santa Rosa, California), Jon Shepard (Nelson, British Columbia), and Jim Troubridge (Langley, British Columbia).

We restrict the type series to specimens from Washington and Oregon because of slight differences in superficial appearance and habitat preferences between these and the California populations. Most California specimens are slightly smaller (forewing length: 14–15 mm) and have more dark filling of the forewing spots than the northern populations. Also, some specimens from San Francisco Bay and Inverness lack most of the black markings and have a dark orange-brown ground color.

Diagnosis: This is the most distinctive species in the *C. cornuta* group; it can usually be recognized without dissection. Males have narrow antennae, 2× as wide as the central shaft, while those of other species are 3× as wide. It is the largest species. Most specimens can be recognized by subtle features of wing maculation: prominent white filling of the forewing orbicular and reniform spots; dark reddish brown forewing ground color; prominent scalloping of the forewing lines; and conspicuous black wedges in the subterminal area of the forewing. Males can be identified by several genitalic features: juxta with a short dorsomedial extension (triangular in the other species); ampulla of clasper short, not reaching the costal margin of the valve (extending beyond the valve in the other species); vesica with one large bilobed and one simple basal diverticulum (two simple diverticula in the other species). Females have an appendix bursae which is smaller than the corpus bursae with the ductus seminalis joining at its posterior end. In other species the appendix bursae is larger than the corpus bursae with the ductus seminalis at its anterior end. Some individuals of *C. gloriosa* from California (vicinity of San Francisco Bay) are lighter in color with reduced black shading, and they lack white filling of the forewing spots. At this locality, *C. gloriosa* might be confused with *C. cornuta*, however, the two species can be differentiated by characters of the male antennae and genitalia described above.

Distribution and biology. *C. gloriosa* occurs in two areas on the Pacific Coast: the Pacific Northwest (Clatsop County, Oregon and Grays Harbor County, Washington) and central and northern California (Humboldt, Mendocino, Sonoma, Marin, Napa, Santa Cruz, and Monterey Counties). Nearly all populations are located near the coastline. In Washington and Oregon it occurs extremely locally in sphagnum bogs within ten miles of the Pacific Ocean. This species has not been found in sphagnum bogs in Pierce or Skagit Counties, Washington or near Vancouver, British Columbia. These bogs differ from those in which *C. gloriosa* occurs in that they are located in an area that was glaciated during the Pleistocene. The types of coastal bogs where *C. gloriosa* occurs might have been more widespread when the sea level was lower, possibly accounting for the current extended distribution of this species along the West Coast. *C. gloriosa* probably occurs further north on Washington's Olympic Peninsula and possibly also in British Columbia. The California populations are not restricted to bogs but occur in mesic forests (Ron Robertson, personal communication).

C. gloriosa is sympatric with the other three species in the *C. cornuta* group, but is the most localized and least common. Adults fly in January to April in California and in March and April in the Pacific Northwest. Both sexes are attracted to lights. The early stages are unknown. The species was recently discovered in California by Ron Robertson and in Washington by the senior author. Additional California specimens were found among specimens of *C. cornuta* in museum collections.

Cerastis enigmatica Lafontaine & Crabo, new species (Figs. 3, 4, 10, 14)

Description. *Male* (Fig. 3): *Head*: reddish brown to dark gray brown; palpi reddish brown to dark gray brown; third segment lighter. *Eyes*: black. *Antennae*: bipectinate, 3× as



13



14



15



16

FIGS. 13–16. Female genitalia of *Cerastis* spp. **13**, *C. gloriosa* Crabo & Laf., Mill Valley, California, CNC 10458; **14**, *C. enigmatica* Laf. & Crabo, Duncan, British Columbia, CNC 110445; **15**, *C. cornuta* (Grt.), Mill Valley, California, CNC 10446; **16**, *C. robertsoni* Laf. & Crabo, Gaviota Pass, Santa Barbara County, California, CNC 11137.

wide as central shaft. *Thorax*: reddish brown to gray brown; collar lighter, buff to reddish tan, with darker transverse lines. *Foretibiae*: spined. *Forewing*: length: 13–15 mm; ground color variable, reddish tan to gray brown, with lighter tints, suffused with variable amounts of black in cell; basal area frequently paler or with more extensive gray scaling than medial or subterminal areas; terminal area paler reddish brown than remainder of forewing; lines double, black with pale filling; basal line faint, sinuous; antemedial line oblique, gently ex-curved, notched basad in fold; median shade usually obscure, when evident a wavy line extending from reniform spot to inner margin; postmedial line scalloped, ex-curved opposite reniform spot, lower half nearly straight; subterminal line weak, pale, undulating, with slender black wedges proximally near costa on radial veins and opposite cell between median veins; terminal line thin, weakly scalloped; claviform spot oblong, black; orbicular spot large, gray or brown, an elongate ellipse, broadly fused with reniform spot; reniform spot large, gray or brown, it and orbicular spot outlined with yellow scales. *Hindwing*: medium to dark fuscous, with darker median shade and discal lunule. *Abdomen*: light gray to reddish brown; untufted, but with long hairlike scales on tergum one. *Female* (Fig. 4): similar to male.

Male genitalia (Fig. 10). Similar to those of *C. cornuta*, except for shape of vesica. Vesica approximately 1.5x as long as aedeagus; distal 2/3 strongly curved, extending first towards left. Two simple subbasal diverticula present. Single cornutus straight.

Female genitalia (Fig. 14). Similar to *C. cornuta* except for bursa shape. Appendix bursae joined to ventral corpus bursae 1/3 from posterior end, extending toward corpus bursae anteriorly.

Type specimens. *Holotype*: ♂: British Columbia: Vancouver, 22 III 1903, ex. coll. Bush Wilson. *Paratypes*: 145 ♂, 19 ♀: ALASKA: Ketchikan, 24–29 IV (1 ♂). BRITISH COLUMBIA: Vancouver Island: Wellington, 2 IV 1903, 27 III 1906 & 4–14 II 1906, Coll. G. W. Taylor (9 ♂, 5 ♀), 25 IV 1903 & 8 & 16 IV 1904, Bryant (5 ♂, 1 ♀), 29 III 1949 & 10 IV 1949, Woodcock (3 ♂); Vancouver Island: Quamichan, 27–28 III 1907, 28 III 1908 & 4 IV 1909, G. B. Day (2 ♂, 2 ♀); Vancouver Island: Duncans, 27 III 1908, 8 IV 1908 & 1–7 IV 1908, Hanham (1 ♂, 2 ♀); Vancouver Island: Mill Bay, 14 VI 1986, K. B. Bolte (1 ♂); Vancouver, 23 III 1903, ex. coll. Bush Wilson (1 ♂), 3 IV 1904 (1 ♂), 192_, W. Downies (2 ♂); Langley, 5 km E, 1–7 IV 1991 & 1–4 IV 1992, J. Troubridge (5 ♂); Queen Charlotte Islands: Massett, 28 V 1894, J. H. Keen (1 ♂); Skagit River Valley, near N end of Ross Lake, 9 IV 1994, J. Troubridge (14 ♂); 16 IV 1994, J. Troubridge and A. & L. Crabo (15 ♂, 2 ♀). WASHINGTON: Cowlitz Co.: Columbia R. valley, 3 mi N of Kalama, SW Carroll's Bluff, 46.05°N 122.86°W, 50 m, 13 IV 1991, L. & A. Crabo leg., disturbed hillside with oak (1 ♂); Cowlitz R. valley, Toutle Rest Area on Interstate 5, 46.35°N 122.90°W, 360', 24 III 1993, L. & A. Crabo leg., lowland forest (1 ♂); Grays Harbor Co.: Ocean City, 26 III 1993, J. Troubridge (1 ♂); North Bay Bog, 0.6 mi N of North Bay of Grays Harbor, 47.05°N 124.09°W, elev. 5 m, 12 IV 1991, L. G. Crabo leg., Native cranberry bog (1 ♂), 26 III 1993, J. Troubridge (5 ♂), 1 IV 1994, J. & L. Troubridge (3 ♂); Humpulips R. valley, Copalis Crossing, 47.10°N 124.07°W, 20 m., 30 III 1992, L. G. Crabo leg., Storefront lights (1 ♂); [Island Co.]: Deception Pass, 27 III 1993, J. Troubridge (1 ♂), 2 IV 1994, J. & L. Troubridge (1 ♂); King Co.: Factoria, 9 IV 1949, E. C. Johnson (1 ♂, 1 ♀); 7.5 mi E of North Bend on Middle Fork Snoqualmie R., 300 m, 47.50°N 121.63°W, 13 IV 1988, leg. L. Crabo (2 ♂, 2 ♀); Kitsap Co.: Bremerton, 1 IV 1948, Don Frechin (1 ♂); Klickitat Co., Columbia River Gorge, Major Creek 1/2 mi N of Columbia River, 9 IV 1994, L. G. Crabo (1 ♂); Mason Co.: Shelton, 16 IV 1949, E. C. Johnson (4 ♂); 2 mi E Little Hoquiam, Grapeview Loop Rd., 25 m, 47.31°N 122.90°W, 24 III 1990, L. Crabo leg. (4 ♂); Elfendahl Pass Rd. 0.3 mi N of Hwy. 302, 2 mi W of Belfair State Park, 47.42°N 122.91°W, elev. 50 m, 29 III 1989, L. Crabo leg. (11 ♂); Okanogan Co., Early Winters canyon, Highway 20 1 mi S of Lone Fir Campground, 7 V 1994, L. & A. Crabo and C. Coughlin (8 ♂); Pierce Co.: Puget Trough, NE corner of Cranberry Lake, 46.90°N 122.36°W, 644', 11 III 1992, L. Crabo leg., native sphagnum bog (6 ♂); [San Juan Co.]: Orcas Island, 18 IV 1949, E. Hendriksen Coll. (1 ♂); Skagit Co., 3.5 mi SE of Big L., Cavanaugh Rd. at Grandstrom Rd., 48.32°N 122.16°W, 550', 14 IV 1993 L. G. Crabo, sphagnum bog (1 ♂); Snohomish Co.: S. Lake Ballinger, 47.95°N 122.32°W, 25 m, 3 III 1988, leg. L. Crabo (2 ♂); Thurston Co.: 3 mi N Tenino, Rocky Prairie, 50 m., 46.89°N 122.87°W, 25 III 1990, leg. L. Crabo (2 ♂); What-

com Co.: Chuckanut Bay of Bellingham Bay, elev. 35 m, 48.69°N 122.49°W, 19 IV 1993, L. G. Crabo leg., dry rock slope (1 ♂); Skagit River Valley near N end Ross Lake, 16 IV 1994, J. Troubridge and A. & L. Crabo (4 ♂); Mt. Baker Hwy. at N Fork Nooksak River crossing, 1/2 mi N of Silver Fir Campground, 23 IV 1994, L. Crabo (19 ♂, 4 ♀); Yakima Co., Tieton River Valley, Oak Creek at Tieton R., 46.72°N 120.81°W, 550 m, 18 IV 1992, L. G. Crabo, riparian forest with oak (1 ♂).

The holotype is in the Canadian National Collection (Ottawa). Paratypes are in the Canadian National Collection (Ottawa), University of California (Berkeley), University of California (Davis), Oregon State University (Corvallis), and the personal collections of Lars Crabo (Bellingham, Washington), Ron Robertson (Santa Rosa, California), and Jim Troubridge (Langley, British Columbia).

We restrict the type series to specimens from Washington, British Columbia, and Alaska.

Diagnosis. *Cerastis enigmatica* is most similar to *C. cornuta* and *C. gloriosa*. It is sympatric with *C. gloriosa*, but can be separated from it by features described in its diagnosis. The male genitalia of *C. enigmatica* differ from those of *C. cornuta* and *C. gloriosa* by the shape of the vesica, which is strongly curved distally, not straight. Females differ from these two species in that the appendix bursae joins the corpus bursae 1/3 from its posterior end, not at the posterior end. Adults are nearly identical to *C. cornuta*, which occurs to the south of the range of *C. enigmatica*. *Cerastis enigmatica* adults tend to be slightly larger with broader wings, they have more contrasting forewing maculation, more prominent light borders surrounding the forewing spots, and slightly lighter hindwings.

Distribution and biology. *Cerastis enigmatica* is moderately common to abundant in mesic conifer forests at low elevations in the Cascade Mountains and on the west coast from the Alaska Panhandle to southern Humboldt County, California (Miranda). It also occurs on the east slope of the Cascades but is much less common there. It occurs with *C. gloriosa* in Washington, Oregon, and at Willow Creek, Humboldt County, California. The adults are active from March to late April at the time when most deciduous trees are in bloom. Both sexes are attracted to light. The early stages are unknown.

C. enigmatica is moderately common in collections but has until now been confused with *C. cornuta*. All previous records of *C. cornuta* from Oregon, Washington, Alaska, and British Columbia are *C. enigmatica*.

Cerastis cornuta (Grote) (Figs. 5, 6, 11, 15)

Pachnobia cornuta Grote, 1874, Bull. Buffalo Soc. Nat. Sci., 2:68.

Type Locality: [California, USA]. [Lectotype in BMNH]

Type specimens. *Pachnobia cornuta* was described from "two fresh specimens" stated to be in the Collection of the Buffalo Society of Natural Sciences. A number of species said to be in that collection (e.g., *Agrotis specialis* Grote, *Agrotis formalis* Grote) have not been found in the collection of the Buffalo Museum of Science but specimens from the Grote Collection labeled "type" and exactly matching the original description are in the Natural History Museum, London. For other species (e.g., *Agrotis wilsoni* Grote) the nominal "type" in The Natural History Museum differ significantly from the description and the types must be considered to be lost. For *Pachnobia cornuta* Grote, a male in The Natural History Museum, London, purchased from the Grote Collection and labeled as a type, matches the description of the species in every detail and is hereby selected as **lectotype**. The specimen is labeled "Type/ California Grote Coll. 81-116/ *Metalepsis cornuta* Grote/ *Metalepsis cornuta* Grote Type."

Diagnosis. Adults of *C. cornuta* (Fig. 5, 6) are nearly indistinguishable from *C. enigmatica* and *C. robertsoni* and are similar to some specimens of *C. gloriosa*. The male genitalia of *C. cornuta* (Fig. 11), *C. enigmatica*, and *C. robertsoni* are indistinguishable except for the shape of the vesica. All three differ from *C. gloriosa* by the presence of a triangular juxta without median extension, longer claspers which extend beyond the dorsal margin of the valves, and the presence of two simple diverticula on the vesica. The distal portion of

the vesica of *C. cornuta* differs from those of *C. robertsoni* and *C. enigmatica* in being straight beyond the basal turn. Females of these three species are distinguished from *C. gloriosa* by having an appendix bursae which is larger than the corpus bursae, with the ductus seminalis joining it at its anterior end. The female genitalia of *C. cornuta* (Fig. 15) differ from those of *C. enigmatica* in that the appendix bursae joins the corpus bursae at its posterior end. They differ from those of *C. robertsoni* in that the corpus bursae is constricted posteriorly, the appendix bursae is even in width throughout its length and projects obliquely away from the corpus bursae anteriorly, and the ductus bursae is shorter, 1.5× as long as wide. *Cerastis cornuta* differs from *C. enigmatica* in slightly smaller size (forewing length: 11–13 mm versus 13–15 mm), less contrasting forewing pattern, and less prominent yellow outline of the orbicular and reniform spots. *Cerastis robertsoni* is slightly smaller (forewing length: 10–13 mm) but is difficult to separate from *C. cornuta* without dissection.

Distribution and biology. *Cerastis cornuta* is moderately common in forests in western California from Sonoma County south to Santa Clara County. It, like *C. gloriosa*, occurs near the Pacific Ocean with most records from the vicinity of San Francisco Bay. It occurs with *C. gloriosa* at a few locations. The adults are active from mid-January through late April. The early stages are unknown.

***Cerastis robertsoni* Lafontaine and Crabo, new species** (Figs. 7, 8, 12, 16)

Description. *Male* (Fig. 7): *Head and palpi*: appearing chestnut (actually a mixture of white, buff, brown, and black scales). *Eyes*: black. *Antennae*: bipectinate, 3× as wide as central shaft. *Thorax*: dark brownish gray; collar pale brownish gray, contrasting with darker head and thorax. *Foretibiae*: spined. *Forewing*: length: 10–13 mm; ground color light to dark brownish gray, suffused with variable amounts of black in discal cell; basal and terminal areas and costa paler gray; lines double, black, pale-filled; basal line sinuous; antemedial line oblique, gently excurved, notched towards wing base in fold; median shade wavy, evident only from reniform spot to inner margin of forewing; postmedial line scalloped, lower half nearly straight, excurved opposite discal cell; subterminal line weak, pale, undulating, with slender black wedges proximally between veins M1 and M2 and near costa on radial veins; terminal line thin, weakly scalloped; claviform spot narrow, black; orbicular spot large, variable, gray, brown, or white, variably outlined with thin pale line, broadly fused with reniform spot and often extended onto forewing costa; reniform spot narrow, oblique, angled towards orbicular spot, gray with partial black and paler gray outline. *Hindwing*: dark fuscous, with darker discal lunule and slight trace of median line. *Abdomen*: gray with long brownish gray hairs; untufted but with numerous long hairs on anterior margin of tergum one. *Female* (Fig. 8): similar to male.

Male genitalia (Fig. 12). Similar to *C. cornuta* except for size of aedeagus and shape of vesica. Aedeagus smaller than that of *C. cornuta*, but with same proportions: vesica approximately 1.5× as long as aedeagus. Vesica bending sharply ventrad 90°, then bent 90° to project to left, distal 2/3 nearly straight. Two simple subbasal diverticula present, one large and one small. Single cornutus straight.

Female genitalia (Fig. 16). Similar to *C. cornuta* except for shape of corpus bursae and length of ductus bursae. Corpus bursae broadly fused with appendix bursae, without posterior constriction. Appendix bursae constricted apically; apical portion curving dorsally to project dorsad. Ductus bursae 2× as long as wide.

Type specimens. *Holotype*: ♂: CALIFORNIA: Monterey Co.: Big Creek Res., UC-NLWRS, 2 II 1994. L. Crabo, J. Powell, & R. Robertson. *Paratypes*: 38 ♂, 10 ♀: CALIFORNIA: Monterey Co.: Chualar, 11 I 1963 (1 ♂); Big Creek Res., UC-NLWRS, Trail to Redwood Camp, 80 m, 24/26 I 1988, J. A. Powell (5 ♂); Big Creek Res., UC-NLWRS, So. Ridge Rd., 220 m, bl. trap, 24 I 1988, J. A. Powell (1 ♂), 28 II 1989, J. Powell & M. Prentice (1 ♂, 1 ♀); Big Creek Res., UC-NLWRS, So. Ridge Pt., 275 m, bl. trap, 24/26 I 1988, J. A. Powell (1 ♂); Big Creek Res., UC-NLWRS, So. Gate Rd., 190–200 m, bl., 24/26 I 1988, J. A. Powell (4 ♂), 21/22 II 1988, J. A. Powell (1 ♂), 28 II 1989, J. Powell & M. Prentice (1 ♂); Big Creek Res., UC-NLWRS, HQ area, 1–10 m, coastal scrub, bl. trap, 24/26 I 1988, J.

A. Powell (3 ♂, 2 ♀), 28 II 1989, J. Powell & M. Prentice (1 ♀); Big Creek Res., UCNL-WRS, 2 II 1994 L. G. Crabo, J. Powell, & R. Robertson (15 ♂, 4 ♀); Santa Barbara Co.: Gaviota Pass, 3 February 1987, Powell & Wagner, blacklight (5 ♂, 2 ♀). An additional 6 males and 1 female from the type locality and Gaviota Pass were examined but were excluded from the type series because of their poor condition.

The holotype is in the University of California (Berkeley). Paratypes are in the Canadian National Collection (Ottawa), the University of California (Berkeley), the University of California (Davis), and the personal collections of Lars Crabo (Bellingham, Washington) and Ron Robertson (Santa Rosa, California).

Diagnosis: *Cerastis robertsoni* is the smallest species of *Cerastis* in North America. It is most similar to *C. cornuta*, which occurs in central California to the north of the range of *C. robertsoni*. *Cerastis robertsoni* tends to have more gray in the forewing, and less conspicuous light-colored outlines of the forewing spots. However, there are no reliable characters for separating these species without dissection. Males of *C. robertsoni* differ from those of *C. cornuta* and *C. enigmatica* by the shape of the vesica: the distal portion of the vesica in *C. robertsoni* extends straight toward the left beyond two 90° basal bends. The female genitalia are most similar to those of *C. cornuta*, but differ by several features: the corpus bursae is broad without posterior constriction; the appendix bursae is broadly fused with the corpus bursae posteriorly and is constricted apically, curving dorsally; and the ductus bursae is longer (2× as long as wide). They differ from those of *C. enigmatica* by having the corpus bursae and appendix bursae joined at their posterior ends. *Cerastis robertsoni* is unlikely to be confused with *C. gloriosa*. However, some specimens have the forewing spots filled with pale yellow, and might mistakenly be identified as *C. gloriosa* using our key.

Distribution and biology. *Cerastis robertsoni* is known only from three localities but may occur more broadly in the Coast Range of central and southern California from Monterey Bay to Santa Barbara County. It is moderately common in California coastal chaparral habitat (J. Powell, pers. comm.) but has seldom been collected, probably because of its flight period early in the year. It is sympatric with *C. gloriosa* at the type locality in Monterey County. Adults are active in January and February. Both sexes are attracted to light. The early stages are unknown.

All but one of the known specimens of *C. robertsoni* were collected by Jerry Powell and his field associates. It was recognized as distinct from *C. cornuta* by Ron Robertson who sent specimens to the junior author for evaluation. We take pleasure in naming this species after Mr. Robertson in recognition of his contribution.

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GENERAL NOTES

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NOTES ON THE SESIID FAUNA OF SOUTHWESTERN WEST VIRGINIA

Additional key words: pheromones, faunal surveys, Appalachian region.

The Sesiidae is a relatively well studied moth family. In the past century, three comprehensive monographs have been written on the group (Beutenmuller 1901, Engelhardt 1946, Eichlin & Duckworth 1988), and several regional surveys have been conducted in the eastern United States (Neal et al. 1983 in Maryland, Sharp et al. 1978 in Florida, Sharp et al. 1979 again in Florida, Snow et al. 1985 in Georgia, Solomon et al. 1982 in Mississippi, and Taft & Snow in 1991 in the north central United States). These studies were aided enormously by the chemical isolation and synthesis of female sesiid sex attractants. In 1974 the synthesis of the (Z,Z)-3,13-octadecadien-1-ol acetate and of the (E,Z)-3,13-octadecadien-1-ol acetate was achieved by Tumlinson and Yonce respectively, and in 1983 the (E,Z)-2,13-octadecadien-1-ol acetate was isolated by Schwartz (Eichlin & Duckworth 1988). The use of these pheromones, alone or in different combinations, in the acetate or alcohol forms, has become the principal method for collecting male Sesiidae and has led to the discovery of many new species and to the elucidation of distributions and flight patterns.

The purpose of the present study is to establish the number of Sesiidae species flying in southwestern West Virginia, and to report on male responsiveness to different synthetic pheromone isomers in "pure" form and in different combinations.

Sampling was conducted over a period of five years, starting in May 1990 and ending in September 1994. Seven locations in two counties were sampled: five in Kanawha County and two in adjacent Putnam County. Three of the Kanawha County locations are situated in the city of Charleston (South Hills, Kanawha City, Coonskin Park). Kanawha State Forest is located at the southern boundary of the city, and Tupper Creek is a small rural community 10 miles north of the city. The South Hills and the Kanawha City locations are densely populated urban areas, with occasional patches of oak woodland. Coonskin Park is a partially developed hilltop that is well drained and rather dry. In addition to the deciduous trees typical for the area, it contains a large population of old pines. Kanawha State Forest is a large tract of undeveloped land containing a variety of microhabitats including gulches, ridges, river bottoms and hills with large tracts of deciduous forest interrupted by small clearings. Tupper Creek is a disturbed area along a small creek with an extensive growth of willow trees. Of the two Putnam County locations, one is situated 20 miles west of Charleston on a fir tree farm, and is surrounded by hills of uninterrupted deciduous forest. The other site, located 25 miles west of Charleston, is a disturbed area on the south bank of the Kanawha River, which supports an extensive growth of willow.

I used Multiplier I traps and lures supplied by the IPM Great Lakes Company (Vestaburg, MI). The lures used in this study are listed in Table 1. In the traps I placed DDVP toxicant strips provided by IPM Great Lakes. In 1990, five traps baited with 97:3, ZZA, EZA, 1:1, and TRI lures were deployed in the South Hills area of Charleston. In 1991, eight traps baited with 97:3, ZZA, EZA, TRI, EZ-2,13-OH, EZ-2,13-A, EZ-3,13-OH, and 99:1 were used on the fir farm in Putnam County. In 1992, 2. eight traps baited with 97:3, EZA, ZZA, 1:1, TRI, 99:1, and EZ-3,13-OH were used in Kanawha State Forest. In 1993, five traps baited with 97:3, ZZA, EZA, 1:1, and 99:1 were used at Tupper Creek and three traps with 97:3, EZA, and ZZA in Kanawha State Forest. In mid June 1993, the 1:1 and 97:3 traps were moved from Tupper Creek to South Hills and the 99:1 trap to Kanawha State Forest. Then, in mid August all traps were moved to Kanawha City. In 1994, three traps baited with 97:3, ZZA, and EZA were used on the Kanawha River shore; three traps baited with 97:3, ZZA, and EZA in Coonskin Park and two traps baited with 1:1 and 2:1 in Kanawha City. At the beginning of August, the three Putnam County traps were moved to Kanawha City.

I began each baiting season in May, when the weather was reliably warm, and ended trapping in late September or early October. In the middle of July I added a new lure load to each trap, making sure that each trap carried the same lure throughout the season; new

TABLE 1. Pheromonal lures used in the present study and their abbreviations. Small percentages of impurities are omitted (these should be less than 1% with current synthesis techniques; Tumlinson 1979).

Abbreviation	Pheromone
97:3	97% (Z,Z)-3,13-octadecadien-1-ol acetate/3% (E,Z)-3,13-octadecadien-1-ol acetate
ZZA	100% (Z,Z)-3,13-octadecadien-1-ol acetate
EZA	100% (E,Z)-3,13-octadecadien-1-ol acetate
1:1	50:50 mixture of (Z,Z)-3,13-octadecadien-1-ol acetate/ (E,Z)-3,13-octadecadien-1-ol acetate
99:1	99:1 mixture of (E,Z)-2,13-octadecadien-1-ol acetate/ (Z,Z)-3,13-octadecadien-1-ol acetate
EZ-2,13-OH	100% (E,Z)-2,13-octadecadien-1-ol
EZ-2,13-A	100% (E,Z)-2,13-octadecadien-1-ol acetate
EZOH	100% (E,Z)-3,13-octadecadien-1-ol
TRI	20:1:3 mixture of (Z,Z)-3,13-octadecadien-1-ol acetate/ (E,Z)-3,13-octadecadien-1-ol/acetate (Z,Z)-3,13-octadecadien-1-ol
2:1	2:1 mixture of (E,Z)-3,13-octadecadien-1-ol acetate/ (E,Z)-3,13-octadecadien-1-ol

toxicant vapor tapes were added at the same time. Traps were placed on tree branches, either at the edge of the forest or on solitary trees, in clearings, at 1–1.5 m above ground with at least 20 m distance between traps. Whenever possible the traps were placed in a south or southwest orientation. I visited each trap once a week and emptied the buckets into labeled styrofoam cups that I took home to record the attracted specimens.

During this study 5080 male sesiids were captured, representing 24 species in 8 genera. Two of these, *Synanthedon kathyae* Duckworth & Eichlin and *Alcathoe carolinensis* Engelhardt, are new records for the state of West Virginia (T. D. Eichlin, pers. comm.). *Melittia cucurbitae* (Harris) was never lured to a pheromone trap but was netted on the foodplant (zucchini squash); since the main purpose of this study was to record as many species as possible for this area, I included it in the present listing. Table 2 lists all the recorded species, showing their yearly abundance at the sample sites. Table 3 gives the monthly distributions and abundances, and Tables 4–5 summarize the sensitivity of male sesiids to the different pheromone lures in this study.

Geographical and temporal trends. The records of *Synanthedon pictipes* (Grote & Robinson), *Podosesia aureocincta* Purrington & Nielson, *Carmenta bassiformis* (Walker) and *Synanthedon rileyana* (Hy. Edwards) show wide year to year fluctuations. Since these four species have at least one generation per year (*S. pictipes* is multivoltine), these fluctuations were probably geographical rather than temporal: one year the traps happened to be placed inside the territory of a population and attracted a large number of individuals; another year they were outside the population's territory and attracted fewer individuals. The number of attracted specimens suggests that these species are abundant inside well circumscribed colonies, which are doubtless centered around their foodplants.

Synanthedon rubrofascia (Hy. Edwards), *Synanthedon scitula* (Harris), *Synanthedon decipiens* (Hy. Edwards), *Synanthedon fatifera* Hodges and *Carmenta ithacae* (Beutenmuller) had similar yearly/geographical fluctuations, but their numbers suggest much smaller and even more circumscribed colonies. It is worth noting the difference in abundance between *Synanthedon exitiosa* (Say) and *S. pictipes*. While these species both utilize wild and cultivated Rosaceae as hosts (Snow 1985, Eichlin 1988), *S. pictipes* appears to be much less abundant and more localized in southwestern West Virginia than *S. exitiosa*.

The records for *Paranthrene simulans* (Grote) and *Paranthrene pellucida* Greenfield & Karandinos confirm their two-year life cycle, with peak numbers being attracted in odd years. In the study area, both species appear to have similar abundance, both peak in the

TABLE 2. Yearly occurrence of sesiid species in southwestern West Virginia based on captures in pheromone baited traps.

Species	Total	1990	1991	1992	1993	1994
<i>Podosesia syringae</i>	1564	67	613	176	488	220
<i>Synanthedon exitiosa</i>	1229	213	168	159	353	336
<i>Podosesia aureocincta</i>	651	3	93	547	7	1
<i>Synanthedon pictipes</i>	519	113	142	9	41	214
<i>Carmenta bassiformis</i>	235	6	2	56	147	24
<i>Paranthrene simulans</i>	181	0	89	4	87	1
<i>Paranthrene pellucida</i>	170	5	95	2	65	3
<i>Alcathoe caudata</i>	127	120	0	5	2	0
<i>Synanthedon rubrofascia</i>	115	33	3	1	17	61
<i>Synanthedon rileyana</i>	110	2	105	2	1	0
<i>Synanthedon scitula</i>	53	1	25	25	1	1
<i>Synanthedon fatifera</i>	29	2	14	0	0	13
<i>Carmenta ithacae</i>	20	0	3	0	0	17
<i>Synanthedon acerni</i>	13	0	2	2	0	9
<i>Synanthedon acerrubi</i>	12	0	11	1	0	0
<i>Synanthedon decipiens</i>	12	0	0	0	2	10
<i>Sannina uroceriformis</i>	12	0	12	0	0	0
<i>Synanthedon viburni</i>	11	3	0	1	0	7
<i>Synanthedon rhododendri</i>	8	0	0	1	0	7
<i>Synanthedon kathyae</i>	3	0	0	3	0	0
<i>Vitacea polistiformis</i>	2	0	0	2	0	0
<i>Alcathoe carolinensis</i>	2	0	0	1	0	1
<i>Vitacea scepiformis</i>	1	0	0	0	1	0
<i>Mellitita cucurbitae</i>	1	0	0	0	1	0

same years, and their two-year cycles occurred in odd numbered years, contrary to Engelhardt's statement (Engelhardt 1946:146) that even numbered years have peak flights of *P. simulans* in eastern United States.

Table 3 shows that the most productive months were June and July. All but one of the 24 species were caught during these two months, the exception being the later-flying *P. aureocincta*. Table 3 also shows distinct temporal segregation of *Podosesia syringae* (Harris) and *P. aureocincta*, the first having peak flight in May and the latter reaching peak flight in September. This lack of overlap is similar to other reports (Eichlin & Duckworth 1988) of an April–May peak for *P. syringae* and a peak after July for *P. aureocincta*. The closely related *P. simulans* and *P. pellucida* also showed a segregation in flight periods. *P. simulans* had peak flight in May, whereas *P. pellucida* peaked in June. Unfortunately, due to unfavorable weather, I never set traps up prior to May; therefore I lack data about the responsiveness of *P. simulans* to sex attractants in even earlier months.

The phenology for *S. pictipes* suggests two generations per year, with a more abundant spring generation in May and June (probably starting earlier) and a less abundant summer generation from July through October. This species is the only one that came to the traps in each month of the study. *S. exitiosa* had an extended flight season as witnessed by other authors (Eichlin & Duckworth 1988, Snow et al. 1985). *S. rubrofascia* exhibited a similar pattern, with a flight period extending from May to September and a peak in July. This matches the data reported by Snow et al. (1985), who were able to capture the moth from April to November in central Georgia. Eichlin and Duckworth (1988) give a shorter flight period (May and June). The specimens captured in this study did not resemble the illustration given by Eichlin and Duckworth in their monograph of the Sesiidae, but, having completely transparent forewings, they matched the illustration given by Taft and Snow (1991).

TABLE 4. Responsiveness of sesiid moths to pheromone lures. Numbers are percentages of the total number of individuals for a given species (sums may not be 100% due to rounding). Numbers in parentheses are the total number of individuals for a given species. No *M. cucurbitae* individuals were taken in the pheromone baited traps.

[illegible]

TABLE 5. Comparison of responsiveness of sesiid species to different pheromone lures in three different studies.

Species	Present Study	Eichlin & Duckworth, (1988)	Taft & Snow, (1991)
<i>P. syringae</i>	97:3, ZZA	ZZA	ZZA
<i>S. exitiosa</i>	97:3, ZZA	ZZA	ZZA
<i>P. aureocincta</i>	97:3, TRI, ZZA	TRI	ZZA, 50/50 ZZA/EZOH
<i>S. pictipes</i>	EZA	EZA	EZA
<i>C. bassiformis</i>	EZA	ZZA, ZZOH	ZZA, 50/50 ZZA/ZZOH
<i>P. simulans</i>	97:3, EZ-2, 13-A	96:4, ZZA	ZZA, 99:1
<i>P. pellucida</i>	97:3, ZZA	no mention	ZZA
<i>A. caudata</i>	TRI	no mention	ZZOH, 1:1
<i>S. rubrofascia</i>	1:1, 2:1 EZA/EZOH	1:1	1:1
<i>S. rileyana</i>	EZ-2, 13-OH	EZOH, EZOH/EZA	EZOH, 50/50 ZZA/EZOH
<i>S. scitula</i>	EZA	ZZA	ZZA
<i>S. fatifera</i>	ZZA, 97:3	ZZA	ZZA
<i>C. ithacae</i>	EZA	ZZA, 97:3	EZA
<i>S. acerni</i>	ZZA, 97:3, light	ZZA, light	ZZA, 50/50 ZZA/ZZOH
<i>S. acerrubi</i>	99:1	EZ-2, 13-A	99:1
<i>S. decipiens</i>	97:3, ZZA	ZZA/EZA, ZZA/EZOH	ZZA, 1:1
<i>S. uroceriformis</i>	EZ-2, 13-OH	EZOH, EZOH/ZZOH	no mention
<i>S. viburni</i>	EZA	EZA	EZA
<i>S. rhododendri</i>	97:3, ZZA	ZZA	no mention
<i>S. kathyae</i>	EZOH, ZZA	ZZA	no mention
<i>V. polistiformis</i>	99:1	99:1	99:1
<i>A. carolinensis</i>	EZA, 1:1	EZA, 3:1	no mention
<i>V. scepisiformis</i>	99:1	ZZA/EZA, ZZA/EZOH	no mention
<i>M. cucurbitae</i>	on foodplant	99:1	99:1

Synanthedon acerni (Clemens) and *Synanthedon acerrubi* Engelhardt had a shorter flight period than given by other sources (Eichlin & Duckworth 1988, Snow et al. 1985, Taft & Snow 1991). Both species were active only in May and June. *Sannina uroceriformis* Walker was active in May and June (see Eichlin & Duckworth 1988, Snow et al. 1985). *Synanthedon viburni* Engelhardt had a more extended flight period (May through August) than *S. fatifera*, which was active almost exclusively in June. *S. scitula*, *S. rhododendri* (Beutenmuller), *S. rileyana*, *S. decipiens*, *C. bassiformis*, *C. ithacae* and *Alcathoe caudata* (Harris) had flight periods similar to those observed by other authors (Eichlin & Duckworth 1988, Snow et al. 1985, Taft & Snow 1991). *A. carolinensis* had an earlier activity period (June and July) compared to other sources (Eichlin & Duckworth 1988, Snow et al. 1985, Sharp et al. 1978). This is somewhat surprising, considering that both Snow's and Sharp's groups collected their specimens to the south of West Virginia (Georgia and Florida, respectively). The flight of *S. kathyae* corresponded with the period given by Eichlin and Duckworth (1988), as did that of *Vitacea polistiformis* (Harris) and *Vitacea scepisiformis* (Hy. Edwards).

Pheromonal responses. The 97:3 blend proved to be the most generalized attractant, yielding a total of 15 species. It was the main lure for seven species: *S. exitiosa*, *P. pellucida*, *P. syringae*, *S. decipiens*, *S. rhododendri*, *P. aureocincta* and *P. simulans*. It also attracted a large percentage of all *S. fatifera*, *S. viburni*, *S. acerni* and *S. scitula*. The "pure" ZZA lure also attracted 15 species but was the main attractant for only two species: *S. fatifera* and *S. acerni* (note that 38% of *S. acerni* individuals were caught at black light, usually early in the morning; this was the only species that came to black light during this

study, see Eichlin and Duckworth 1988). The "pure" EZA pheromone was attractive to 11 species; for six of those it was the main attractant: *C. ithacae*, *S. pictipes*, *S. scitula*, *C. bassiformis*, *S. viburni* and *A. carolinensis*. Surprisingly, the TRI mixture was only moderately attractive for *P. aureocincta*, for which it was originally formulated (Nielsen et al. 1979), attracting only 21% of the 651 individuals of *P. aureocincta* caught. In contrast, 59% of the individuals responded to the 97:3 mixture. Sharp and Eichlin report the same weak attraction of this combination for *P. aureocincta* (1979).

The TRI lure proved strongly attractive to *A. caudata* (92% of the total). *A. caudata* displayed a specific pheromone responsiveness: of 120 specimens caught in 1990 in South Hills, 117 responded to the TRI lured traps and only three to the 97:3 traps. In 1991 no individuals came to the TRI trap in Putnam County. In subsequent years I did not have the TRI lure, but the 97:3 lure attracted 5 and 2 individuals respectively in Kanawha State Forest and Tupper Creek. This suggests that *A. caudata* occurs in large, well circumscribed colonies, and the individuals exhibit a strong attraction to the TRI mixture. *Synanthedon acerrubi* Engelhardt and *Sannina uroceriformis* Walker exhibited the same geographical confinement, but the numbers caught indicate small colonies or weak responses. The 1:1 mixture attracted *S. rubrofascia* (76% of the total). The 99:1 blend lured all the *V. polistiformis* and *V. scepiformis* caught and was highly attractive for *S. acerrubi* (83% of the total). EZ-2,13-OH was a highly specific lure for *S. uroceriformis*, (100% of the total). It also proved attractive to *S. rileyana* (83% of the total). The EZOH isomer was a less effective attractant for *S. rileyana* (10% of the total), and lured two individuals of *S. kathyae* (66%). No *M. cucurbitae* males were attracted to any pheromone traps, even though a 99:1 baited trap was kept close to the patch with zucchini-squash plants, where the only individual caught during this study was netted.

Table 5 summarizes male sesiid responsiveness to different sex lures in three different studies: the present work, Eichlin and Duckworth (1988) and Taft and Snow (1991). In the present study *C. bassiformis* exhibited a strong affinity toward the EZA lure (77% of the total), whereas the other two studies reported the ZZA isomer as most attractive. Since these were the same EZA baited traps that attracted 94% of *S. pictipes* individuals, and since it is known that the presence of as little as 1% of the ZZA isomer as an impurity would significantly reduce the response of the moth to the lure (Tumlinson 1979), it can be concluded that the EZA lure used in this study was of high purity. The same scenario occurred with *S. scitula*: 80% of the individuals in the present study came to the EZA traps, while the other studies found the ZZA isomer to be the main lure. It would be interesting to find out if circumscribed and geographically isolated populations of the same species could be responsive to different pheromone isomers (there is some indication that attractancy to pheromones or mixtures may vary depending on what other species fly in the same area; Eichlin, pers. comm.).

In conclusion, with 24 species recorded here, southwestern West Virginia appears to have a rich sesiid fauna. Further collecting will doubtless add more species to the list (while this paper was being prepared, a male *Synanthedon sigmoidea* (Beutenmuller) was taken at Kanawha City in a 99:1 trap). The abundance data reported here should be interpreted with caution: pheromone bait trap captures of males in specific locations may or may not reflect the overall abundance of particular species in the whole region. For instance, *M. cucurbitae* is certainly a common species in southwestern West Virginia where host plants are available, yet no individual was caught in any of the baited traps. It would be erroneous to conclude from this study that *M. cucurbitae* is a rare species.

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MIGRATORY ACTIVITY IN *VANESSA CARDUI* (NYMPHALIDAE) DURING 1992 IN WESTERN NORTH AMERICA, WITH SPECIAL REFERENCE TO EASTERN CALIFORNIA

Additional key words: migration, population dynamics, weather, Owens Valley.

Migrations of *Vanessa cardui* (L.) were unusually large in southwestern North America during 1991–1992, the largest since 1968 and 1973, providing a rare opportunity to study the complex mass behavior and population dynamics of this species (cf. Woodbury et al. 1942, Abbott 1951). Here we summarize 1992 records for the region and present observations made by one of us (DG) in Inyo County, California. The methods follow those outlined in Giuliani and Shields (1995). Migration rates here (no./5min/15m) are arbitrarily classified as light (1–29), small-scale (30–49), medium-scale (50–99) and large scale (>99). *Vanessa cardui*, like the monarch (*Danaus plexippus* L.), has a southward return migration during the summer and fall (Emmel & Wobus 1966, Shapiro 1980, Myers 1985, Nelson 1985, Giuliani & Shields 1995).

Small numbers of migrating *V. cardui* were reported during February and March 1992 in California, including: NW at Hemet (29 February, 12–22 March), NNW in San Diego County (9–10 March), NW–WNW near Bakersfield (11 March), NNE–WNW in Inyo County (15–17 March), and WSW in Ventura County (19 March) (pers. obs.; J. F. Emmel, in litt.; McKown 1993). A light migration was seen between Barstow and Yucca Valley on 26 March (McKown 1993). Many northward migrators were seen near San Diego (27–30 March) (R. Larson, pers. comm.), and there were several newspaper accounts of *V. cardui* plastering windshields during late March in the southern San Joaquin Valley.

One of us (DG) toured SE California and extreme W Arizona during 19–28 March to monitor *V. cardui* activities. Sightings increased southward from only a few non-migrators at NW San Bernardino County to a large-scale migration at Mecca, Riverside County; light to small-scale flights occurred in Imperial County and SW Arizona. Directions observed varied from NNE to W with most flights headed NNW–NW.

On 28 March, R. E. Wells (in litt.) observed *V. cardui* in Baja California from Catavina to 5 km N Los Angeles Bay cutoff, where thousands of larvae were feeding on *Malva* L. (Malvaceae) with pupae utilizing the spines of young cardon cacti. Migration flights to the NNW were noted from Los Angeles Bay cutoff to 40 km SE Guerrero Negro. At San Lucas Cove during 28 March–6 April, adults flew NW–NNW, including 11 km offshore. On 9 April a large NNW–NW migration (3–30/km and over 300/min counted while driving) was seen in the vicinity of Guerrero Negro to ca. 65 km SE of there. Near Rosarito, up to 93/km were counted and numbers increased near Punta Prieta on 9 April to an estimated 620+ km, with larvae evident on the highway.

Vanessa cardui significantly expanded its range northward during April. In Little Chino Valley (Yavapai County, Arizona), fresh adults migrated NW on 6–7 April in uniformly large numbers over at least a 16 km front; the main flight period lasted for 5 h each day (L. Muehlbach, in litt.). Migrations near Phoenix were completed by 10 April, with heavy NE movement in NE Arizona and NW New Mexico during 15–20 April even under cold, cloudy and snowy conditions; large sedentary populations were present during late April and early May in the North Rim, the Flagstaff area, and in the White Mountains (K. Roever, in litt.). A large flight passed through Denver, Colorado in an ENE–NE direction during 26 April–5 May (Scott 1992). Large numbers flew in the Los Angeles area in early April (M. & S. Foster, in litt.) and on 13 April in the western Mojave Desert (R. Larson, pers. comm.). There were nearly daily migrations in Inyo County throughout April, some large-scale in size, and migrations first appeared in Mariposa County after 5 April. Many migrating *V. cardui* were present by mid April in the Davis–Sacramento–Reno area, as well as in Salem, Oregon (R. Wescott, in litt.). On 27 April, large numbers flew SW in Owyhee County, Idaho (McKown 1992), and many faded migrators reached extreme SW British Columbia on 25–28 April (C. Guppy and R.P. Nelson, in litt.). From May to August, *V. cardui* became widespread in the United States and southern Canada (cf. McKown 1993, Swengel & Opler 1993).

Inyo County observations. The first *V. cardui* appeared 3–17 March at Big Pine and displayed no apparent migratory behavior, as 3–6/day nectared on the blossoms of apricot trees. Light to large-scale migrations were seen 4–25 April at various Inyo County locations, with no migrations during 26–30 April. Beginning in May, flights became more complex as NW migrators intermingled with locally emerging adults that also flew northward. Occasional migrators appeared 1–3 May as local emergence began, soon producing densities comparable to those of April. Light to large-scale migrations were observed 4–17 May, with a lull on the 13th. Few were seen during 18–21 May, but numbers increased in the following week (including two large-scale flights). Subsequently, few migrated on the Owens Valley floor, though light migrations continued at higher elevations in Inyo County until early October.

Table 1 summarizes the numbers and directions taken by migration flights through Owens Valley during the spring of 1992. These flights reached maximum densities in mid-April and largely represent an influx from the SE, from the direction of the Sonoran Desert region of SE California, S Arizona and NW Mexico. Table 2 summarizes the large densities achieved by some of the migratory flights in the Inyo County region during April and May 1992.

The final large-scale migration of *V. cardui* in Inyo County occurred on 25 May at 1980–2315 m in the Inyo Mountains, with up to 152/5 min/15 m flying N–NE in the late morning. Migration rates were low below 2990 m 26–31 May, with almost no migrators at Big Pine after 1 June. Occasional migrators were observed at higher elevations through June, with small numbers also on flowers.

Fig. 1 shows the shift in migratory flight directions during the summer. Southward migration began in early July, overlapping with residual NW movement, and continued into October. These southward flights consisted of small numbers (<1/5 min/15 m) primarily at

TABLE 1. Spring migrations of *Vanessa cardui* through Owens Valley, Inyo County, California in 1992.

Date	Maximum #/5 min/15 m	Primary Geographic Directions
March 17	1	NW-WNW
April 1	2	NNW-NW
April 3	2	NW-WNW
April 4	9	N-W
April 5	59	variable (E-N-SW)
April 7	30	NW-SW
April 8	62	N-NW
April 10	228	NW-W
April 14	19	NNE-NW
April 15	81	NNW-WNW
April 16	265	WNW-WSW
April 21	179	NW
April 22	83	NW-WNW
April 23	50	NNW-WNW

high elevations (less than 20% of the observations were below 3000 m). Only one migration of 1992 showed a clearcut change of direction with time of day. On 5 April at Big Pine, 0800–1200 h, under clear skies and no wind, a medium-scale migration initially heading NW altered its direction counter-clockwise at a steady rate of 27°/h until heading SW as the sun moved clockwise across the sky.

In Saline Valley at 480 m on 16 and 26 November, occasional individuals were seen in flight and on *Baccharis* flowers. No adults were seen in Saline Valley on 23–27 December under mostly sunny conditions with no wind (in some years a few have been seen there throughout the winter). Elsewhere, a few nectaring adults were observed 20–21 September in the Providence and Dead Mountains, San Bernardino County, and several adults were seen on *Lantana* flowers at Hemet in November (J. F. Emmel, in litt.). On a trip to Baja California Norte in late November-early December, R. E. Wells (in litt.) observed only one adult at Miller's Landing.

TABLE 2. Inyo County, California large-scale migrations of *Vanessa cardui*, 1992.

Date	Locality	Elev (m)	Time (h)	#/5 min/15 m	Primary Directions
April 10	Lone Pine	1130	0830–0845	206–228	NW-W
April 16	8 km E Big Pine	1435	0920–0955	124–265	WNW-WSW
April 16	Deep Springs Valley	1615	1300	128	SW-SE
April 17	Gilbert Summit	1890	1245	135	SE (some NW)
April 17	Gilbert Summit	1980	1400–1425	116–139	WNW (some SSE)
April 20	N end Eureka Valley	1260	0645–0700	266–351	NW
April 20	E of Big Pine	1830	1500	845	NW-WNW
April 21	White Mountains	2805	0815	104–105	NNE-NNW
April 21	White Mountains	2650	0845	427	N-NW
April 21	Big Pine	1220	1145	179	NW
May 6	Crater Mountain	1830	0900–1100	>295	N
May 10	Bridgeport, Mono Co	1970	0800	100	WNW-WSW
May 12	White Mountains	2195	0745–0803	100–329	ENE-NNE
May 17	N end Death Valley	1495	0830–0840	130–131	SE-ENE
May 24	Inyo Mountains	2315	0945–1125	122–281	NNE-NW
May 25	Inyo Mountains	2135	1115	152	NE-N

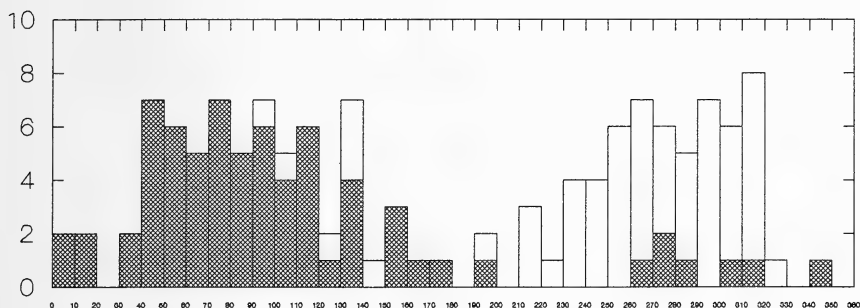


FIG. 1. Stacked bar chart showing change in flight direction from north to south of *Vanessa cardui* migrations above 2745 m in Inyo County, California. Black = May 12 to June 10, 1992; white = July 3–19, 1992. All directions are geographic: east = 0, north = 90, west = 180, south = 270. Vertical axis shows number of individuals observed within each 10-degree interval.

Mariposa County observations. *V. cardui* were first seen in Mariposa County migrating NNW–NW, on 6–8 April near Mariposa, with a medium-scale migration flying NW on 9 April (1530–1645 h). On 19 April, NW migrating reached rates of 35–65/5 min/15 m at 1035–1205 h, decreasing to occasional migrators on 20 April. A few dozen nectared at blossoms of *Brodiaea* Sm. (Amaryllidaceae) as well as yard *Buddleja* L. (Buddlejaceae) and apples. At Mariposa migration ceased whenever cloud cover appeared.

At 1100 m at Jerseydale, *V. cardui* migrations did not appear until 21 April when a large-scale migration of worn individuals flew NNW at about 1400–1500 h. On 3–4 May occasional migrators occurred, along with resident *V. cardui*, that oviposited on lupines, *Rumex* L. (Polygonaceae), and other annuals. On 4 May at 1430 h, a small-scale migration of mostly fresh individuals flew NNE–NNW; flight was mainly to the NNE at 1530–1615 h with numbers decreasing by 1645 h, and ceasing at 1743 h (occasional individuals flew in the opposite direction at 1726 and 1734 h). On 5 May at Jerseydale, migration began at 0755 h in partly cloudy weather, with very few migrating at 0900–1000 h under overcast skies, with many nectaring on *Chamaebatia foliolosa* Benth. (Rosaceae). Only a few adults were seen after late May: on 9 June, 4 July, 25 July, and 11–13 October. On 11 June 10–15% of the meadow thistles (*Cirsium*) had larval web-nests with dried frass of all sizes, but only four medium to large larvae were located (two alive, two dead). No larvae were found on lupines or other plants despite the earlier large migration numbers.

At Jerseydale, six migrators were captured on 5 May and were placed at one location in the grass at the end of the day. These remained torpid overnight and began activity on 6 May between 0640–0800 h by first rapidly vibrating their closed wings for about 2–5 minutes; four of the six then flew in a complete circle before heading off erratically in a flight direction before usually landing again, while two others took off immediately without a circle flight. The weather was overcast with dilute sunshine and calm conditions. Possibly the circling flight was performed for initial sun-orientation during overcast weather. In late April 1941 at 0650 h, six migrators that spent the night on a lawn flew up, circled around, and flew off to the NW (Abbott 1950:166).

Migration times. No migrators were seen before sunrise. In Imperial County, as the sun was rising on 24 March at 0600 h, *V. cardui* adults were easily disturbed from the ground, with the first migrators observed at 0623 h; they appeared to first warm up on the ground at dawn, then went to flowers, then migrated. On 20 April in Inyo County, a single migrator was observed at 0555 h and another at 0600 h; at 0645 h a large-scale NW migration abruptly appeared. Atop a 2315 m ridge in the Inyo Mountains on 24 May, counts were made of a large migration from 0500 to 1800 h. The first migrators were seen at 0545 h and the last at 1735 h. The rate during successive 2-hour times from 0700 h was 14, 75, 235, 52, 10; an estimated 517,000/km passed through the area on that day.

Cessation of daily migrations was determined in only a few instances. On 5 April a medium-scale migration at Big Pine continued until about 1705 h. On 9 April in the Owens Valley, occasional *V. cardui* were still migrating well after sunlight (until 1845 h) had left the tops of the surrounding mountains; four more were observed close together in flight against the moonlit clouds after 1900 h (D. Constans, pers. comm.). A medium-scale migration on 16 April ceased flying between 1725–1735 h. On 9 and 19 April at Mariposa, migration ceased at 1727–1730 h. On 9 May at Reno, Nevada, occasional migrators were last seen about 1800 h.

Wind effects. On 22 April near Bishop a migration flew mainly NW during calm conditions, many 3–6 m high and a few up to 30 m high. Later, when strong gusty winds from the N were present, they all flew within 0.6 m of the ground, rising higher whenever the winds abated. Other reports have noted *V. cardui* migrations flying low to the ground against stiff or near gale-force winds (cf. Woodbury et al. 1942:172, Giuliani 1977).

At 0900–1100 h on 6 May at an 1830 m summit south of Big Pine a large-scale migration flew N off the top under a light S wind. Most were initially 1 m above the ground but continued flying horizontally or slightly upward as they poured over the summit, instead of descending down slope. Similar behavior in migrating *V. cardui* over hill and mountain summits has been reported elsewhere (cf. Wright 1906:37, Shields 1967: 112). On 23 May, atop a 2315 m ridge SE of Big Pine during a medium-scale migration with winds from the ESE–SSE, adults flew mainly NNE–NW up slope and continued upwards at the angle of the slope after passing the crest.

When flying in a strong crosswind, individuals are often oriented to as much as 45° away from the observed direction of motion (toward wind direction).

High fliers. Although most migrations stayed within 5 m of the ground, some high altitude flight was observed. On 23 March at Coachella, Riverside County, at 1200 h, a small-scale migration proceeding NW–WNW flew 1.2 m to over 30 m high during warm, cloudy, breezy conditions. High-fliers proceeded in the same directions as those lower down. Flight numbers fluctuated dramatically, probably caused by the cooler cloud shadows encountered along their route. On 5 May near Big Pine, 0900–1100 h, under heavily clouded conditions, a light migration went N–NW; on four different occasions, individuals flying at under 2 m high climbed at a constant 20–40° angle until out of sight, while occasional migrators were seen fluttering or drifting at 15 m to over 30 m high.

On 16–17 April at the SE base of a steep 700 m high ridge east of Big Pine, a large NW migration occurred under both heavy cloud cover and mostly blue sky conditions, extending up to at least 300 m above the ground. Numbers observed by binocular reached as much as 600/min: many appeared to be drifting, hardly fluttering their wings, as though allowing themselves to be carried NW by the wind. Some of these drifters were spinning slowly (like drifting leaves) with no attempt to maintain a constant orientation. On the summit of this ridge, migrators came over the top no more than 15 m high. A similar case was noted on 24 May atop a 2315 m ridge SE of Big Pine when drifters were seen to over 100 m high at 1715 h under a cloud shadow; they did not move their wings and often were rotated about so that they faced many different directions (including opposite to the direction of movement). High flying in *V. cardui* appears to differ from that observed in migrating *D. plexippus* (see Gibo 1986, Gibo & Pallett 1979) i.e., directed ascending flight vs. gliding in circles in rising air currents, although both exhibit some passive drift-gliding in tail winds aloft.

Interactions. Occasional interactions by individual *V. cardui* on the ground toward migrators were observed. Seen most frequently in late afternoon or dusk and occasionally in the early morning, individuals would rise from the ground to follow or interact with a migrator and then return to the same spot. On 25 March in San Bernardino County, walking at dusk caused adults to rise from the ground, including an occasional pair that flew up close together and then settled back down to the ground together.

Pairs were often present in a migration, usually as one individual flying directly behind another. Seen from March through May, primarily during late afternoon or morning hours, they constituted as much as 10% of the total numbers in flight (over 50% on one occasion). The sex(es) of such pairs could not be determined, however.

Courtship. Several courtships involving *V. cardui* were seen late in the day during

mid-April in Inyo County, though no actual matings were observed. On 11 April at 1615 h in strong winds, a pair descended to the ground and the male approached the female; the female avoided the male's approaches, crawled into the base of a shrub, and the male perched on a twig 1.5 cm above her. On 17 April, after 1600 h, one pair landed in a shrub and each time the male approached, the female fluttered a few cm away. After the fourth try the male flew out and landed on the ground 1 m away. The female then immediately came out from inside the shrub and flew, sweeping low over the male, and the male rose and followed. Brown & Alcock (1990) reported four *V. cardui* pairs courting at 1605–1650 h on a central Arizona hilltop; two mating pairs of *V. cardui* are recorded for 1800 h (Shields 1967, Brown & Alcock 1990); and two matings of the closely related *V. kershawi* (McCoy) occurred at 1730 h in Australia (Alcock & Gwynne 1988).

Puddling. On 27 April, mostly very worn adults were fairly numerous on moist soil beside a creek. On 17 May in the Inyo Mountains during a large migration that progressed NNE, many were imbibing at muddy soils created by an irrigation ditch (D. Howell, pers. comm.). Similarly, during a heavy migration in late May 1941 near Price, Utah, large numbers congregated around roadside puddles (Knowlton 1954). Puddling behavior is known to replenish sodium and water loss in male butterflies (Adler & Pearson 1982).

Nectaring. *V. cardui* utilized many native desert flowers as nectar sources. In approximate descending order of preference among the most readily used species were: *Prunus andersonii* Gray (Rosaceae), *Dalea fremontii* Torr. (Fabaceae), *Salix* L. (Salicaceae), *Amsinckia tessellata* Gray (Boraginaceae), *Encelia virginensis* A. Nels. (Asteraceae), *Tetradymia* DC. (Asteraceae), and *Stanleya elata* Jones (Brassicaceae). In the Owens Valley on 13 April an estimated 6000 adults were observed nectaring on a patch of *P. andersonii* 6 m in radius, and at Keeler on 10 April many thousands from a migration neared on the numerous introduced *Tamarix* L. (Tamaricaceae) trees that were in full bloom.

Oviposition, dwarf adults and hostplants. The large migrations of early April produced many eggs throughout Inyo County, primarily on the abundant *Amsinckia*. During 15–17 April, *Amsinckia* plants were found with up to 21 eggs per leaf along with small numbers of first instar larvae. By 19–21 April, many sites had more young larvae than ova. Small to dwarfed adult *V. cardui* were common in May 1992, likely the result of their annual foodplants, such as *Amsinckia* and *Cryptantha*, drying out earlier than usual (i.e., in contrast, migrating adults in Inyo County during April and after May were mostly normal and large sized). At most sites in the Owens Valley, *Amsinckia* germinated during December 1991 and had already advanced to the blooming stage by the time migrators arrived and oviposited in early April. By late April, the plants had mostly dried out and larvae were in instars 1–3 (few larvae or pupae could be found by 7 May). Millions of larvae likely perished there during late April due to the desiccation of the *Amsinckia* fields.

On 18 April in the Chemehuevi Mountains, San Bernardino County, *V. cardui* larvae were abundant on *Plantago insularis* Eastw. (Plantaginaceae) with others on *Amsinckia* and *Cryptantha*, with fresh to worn adults common that were about 50% dwarfed (J. F. Emmel, in litt.). On 3–4 May, Emmel noted many nectaring adults near Amboy and in the Providence Mountains, San Bernardino County (also about 50% dwarfed). On 4 May at Jerseydale, Mariposa County, the junior author observed many small to dwarfed adults in a small-scale migration heading NNE in the late afternoon, most appearing fresh. Many adults of medium-small to dwarf size occurred in Inyo County from about 6–30 May. Dwarfs were common in Iron and Washington Counties, Utah, on 22–23 May, with a statewide dwarf population present in Colorado in late May (McKown 1993).

V. cardui larvae were found in 1992 on the following hostplants that are additions to those reported for 1991 (Giuliani & Shields 1995): Boraginaceae: *Cryptantha angustifolia* (Torr.) Greene, *C. circumscissa* (H. & A.) Jtn., *C. gracilis* Osterh.; Fabaceae: *Lupinus concinnus* var. *orcuttii* (Wats) C.P. Sm., *L. flavoculatus* Heller, *L. inyoensis* Heller, *L. magnificus* Jones, *L. pusillus* var. *internontanus* (Heller) C.P. Sm. A number of new hostplants were also recorded for the northern Central Valley of California in 1992 (Witham 1991).

Crawling larvae. On 24 April at 670 m at the NW edge of Panamint Valley, *V. cardui* larvae were abundant in an area where *Amsinckia* and *Cryptantha* plants were heavily eaten and desiccating. Many were crawling in straight lines on the ground in the morning,

in roughly the same densities regardless of substrate and topography. Crawl speed averaged 1–2 m/min at densities up to 10/min over a 1 m line; two larvae crawled, respectively, 11 and 18 m in 10 min and neither deviated more than 5° from a straight line. Though all possible crawl directions could be found, about 80% were going ENE–NNE and 20% WSW–SW with only a few in other directions. Larval measurements indicated that 2nd–5th instars were involved in crawling (see Hammad & Raafat 1972) while many 4th and 5th instars remained on plants. While crawling, larvae often paused at plants they encountered, investigated the leaves, and fed for varying lengths of time if it was a hostplant. If it was not a host, they continued crawling in their fixed directions. By 1000 h, with rising ground temperatures, crawlers developed a strong tendency to leave their linear paths and head toward large objects (such as the observer), and most larvae soon ascended into *Cryptantha* and *Amsinckia* plants. However, many 3rd or 4th instars at this time were feeding on the leaves of *Mentzelia*, a plant they do not normally eat.

Predators and parasites. In mid-April along the highway between Big Pine and Bishop, Inyo County, crows picked up dead and injured *V. cardui* adults that had been hit by cars (one had several in its beak). On 5 May at Big Pine, three english sparrows were pulling larvae off *Amsinckia* plants and eating them. On 24 April, black harvester ants were seen carrying off small, living larvae. On 5 May near Big Pine, over a dozen of a large unidentified wasp were searching *Amsinckia* plants and attacking any larvae they found. On 16 May at Owens Lake, a yellow-green crab spider, on a flower matching its color, had captured an adult (*D. Constans*, in litt.). On 2 July at 2745 m in the White Mountains, 11 small pupal cases of a wasp were found near where small larvae had been, in hidden and webbed locations between overlapping leaves of *Cirsium drummondii* T. & G. (Compositae).

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DANCING WITH FIRE: ECOSYSTEM DYNAMICS,
MANAGEMENT, AND THE KARNER BLUE
(*LYCAEIDES MELISSA SAMUELIS* NABOKOV) (LYCAENIDAE)

Additional key words: conservation, endangered species, metapopulation dynamics, sand and oak barrens, savanna, prescribed burning.

The recent listing of the Karner Blue Butterfly (*Lycaeides melissa samuelis* Nabokov) as an endangered species (Clough 1992) has increased interest in managing and restoring populations of this charismatic invertebrate. The Karner Blue and other lepidopteran species are rapidly becoming symbols for restoring and conserving the barrens/savanna ecosystems that occur on well drained sand deposits in the Great Lakes Region and New England. The dynamic processes that produced unique botanical communities also produced a highly specialized community of invertebrates adapted to this regime. Because of their general biological requirements, invertebrates are often closely linked to a few key ecological resources, such as specific soil types, edaphic conditions and/or individual host-plant species or genera (Panzer et al. 1995).

The importance of oak barrens/savanna habitats to invertebrates is well illustrated by the Lepidoptera. In Ohio, the only midwestern state with a completed state-wide survey of all Lepidoptera species, the Oak Openings, Ohio's only oak barrens/savanna community, supports the largest assemblage of imperiled butterflies and moths in the state. For example, five species of imperiled butterflies and 17 species of owlet moths (Noctuidae) occur in the Oak Openings, representing approximately 4% and 3% respectively, of the resident species in Ohio (Shuey et al 1987a, 1987b, Metzler & Lucas 1990, Iftner et al. 1992, Rings et al. 1992). The maintenance of this ecosystem is vital for the preservation of lepidopteran



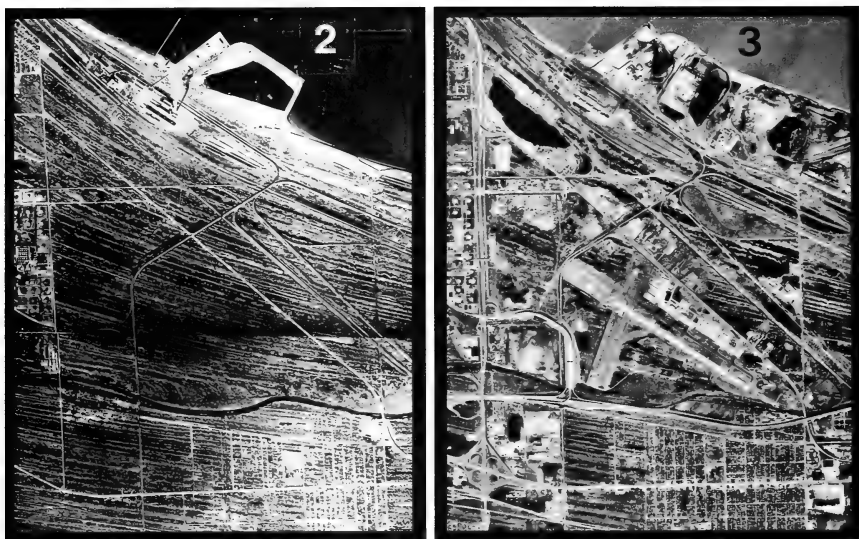
FIG. 1. Karner blue habitat: oak barrens in Newago County, Michigan. Note the sunlit, grass-dominated opening surrounded by oak woodlands and numerous, fire-stunted oak and jackpine saplings within the clearing.

biodiversity, as well as for other lesser known plants and animals in Ohio and the importance of oak barrens/savanna communities to biodiversity maintenance in the other Great Lakes States is certainly similar to the situation in Ohio. For example, Panzer et al. (1995) list 17 species of butterflies that are primarily restricted to sand prairie, savanna and xeric prairie in the greater Chicago region.

The decline of oak barrens/savanna lepidopteran communities can be attributed to several factors, but habitat loss, the disruption of ecosystem level processes and patch dynamics, and the collapse of metapopulation dynamics of many species are generally the primary contributors. Here I discuss these intertwined processes, and the management implications and problems associated with each process as they relate to the Karner Blue (for ecological information regarding other imperiled midwestern lepidopteran species, see the species and habitat accounts in Rings et al. 1992 and Iftner et al. 1992).

Habitat loss and fragmentation resulting from physical alteration. Habitat loss is often the most easily implicated factor contributing to the decline of most imperiled invertebrate species (Hafernik 1992) and the Karner Blue is no exception. To persist locally, Karner Blue populations require relatively large stands of the hostplant, blue lupine (*Lupinus perennis* L.) (Opler & Krizek 1984). Habitats supporting the butterfly are generally open and sunny with scattered trees and shrubs (Fig. 1), and are dominated by grasses and other herbaceous species growing in well drained, sandy soils—in other words, healthy barrens/savanna communities (Zaremba & Pickering 1994). Oak barrens/savanna loss can be attributed to several factors, ranging from outright destruction to more subtle secondary impacts such as the encouragement of forest growth in areas of urban encroachment.

Oak barrens/savannas have been subject to the same trends that altered almost every ecosystem in eastern North America. The expansion of agriculture into new ecosystems was largely a process of trial and error: farming sand barrens was an error. In the trial process, many habitats were altered or destroyed and the local hydrology was often modified.



FIGS. 2–3. Fragmentation of the dune and swale ecosystem (including dune-top oak barrens) of southern Lake Michigan. **2**, the system in 1938. **3**, the system as it appeared in 1994. Note the fragmentation and almost complete isolation of the remaining dune and swale fragments, surrounded by urban/industrial Gary and Hammond, Indiana. Scattered throughout this complex are habitats that support or have the potential to support the Karner blue. Fig. 2 courtesy of the Indiana Geological Survey.

This trial process came to a halt during the prolonged drought of the 1930's, when it became apparent that the infertile soils of these communities could not support sustainable agricultural production.

The unfortunate location of many regional barrens/savanna communities also contributed to their destruction, especially in New England. For example the Albany Pine Barrens sit adjacent to the city of Albany, New York, and the expansion of the city has, and still is contributing to the urbanization of this ecosystem (Dirig 1994). The Oak Openings ecosystem in Ohio is suffering the same fate as Toledo suburbs expand (Iftner et al. 1992, Grigore & Windis 1994); And the complex dune and swale communities which once lined southern Lake Michigan have been almost eliminated by industrialization and urbanization (Figs. 2 and 3).

On a broader scale, the infertility of the sand soils themselves has led to the destruction of sand barrens communities. Many abandoned farms located in oak barrens/savanna ecosystems eventually reverted to federal and state ownership (via tax defaults), largely to become public forest land. Because the preservation of non-forest communities was not a high priority of national or state forests in the 1930's through the present, many oak barrens/savanna communities were converted into 'productive' use by conversion to pine plantations. These monocultures of stressed trees bear witness to the incomplete and short-sighted ecological planning of past eras. Degraded barrens communities continue to be primary targets for new developments such as industrial parks and residential communities, possibly because the cost associated with acquiring barrens land is less than the cost for purchasing 'productive' agricultural lands.

Habitat loss and fragmentation resulting from the disruption of ecosystem level processes and patch dynamics. Closely related to the impact of habitat loss is the elimination of ecosystem level processes. Oak barrens/savanna communities are among the most dynamic in the Midwest—the open habitats that support the Karner Blue

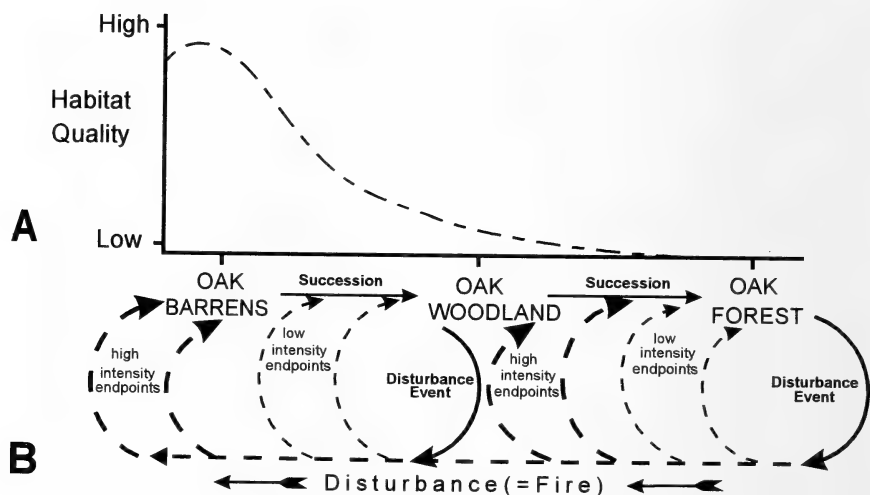


FIG. 4. A simple model of the interaction between Karner blue habitat suitability, oak barrens succession, and fire disturbance. **A:** Optimal Karner blue habitat is early successional oak barrens; as succession proceeds, habitats become shaded and habitat quality decreases. **B:** Oak barrens, in the absence of disturbance, convert through succession to oak woodland/oak forest communities. Note that while fire and other disturbances can re-set succession to an earlier state, the exact outcome depends upon fire (disturbance) intensity and other mitigating factors. In the absence of disturbance, Karner blue habitat is eventually lost.

were originally maintained by a steady procession of wildfires, which killed woody invasive plants while favoring fire-adapted dune and savanna communities. Without fire disturbance, shade tolerant and fire sensitive species increase in density, and open barrens and savanna species decline.

Functional oak barrens/savanna communities are in a constant but dynamic flux. Succession pushes the community towards an association characterized by fire intolerant woody and shade tolerant herbaceous species, while fire disturbance realigns the community towards fire tolerant and shade intolerant species (Fig. 4). The original patch dynamics of these communities was in constant flux, and individual sites supported communities that reflected recent disturbance history. Although fire may have been a yearly occurrence within oak barrens/savanna ecosystems, the spatial distribution of the fire was less predictable. For example, in the Albany Pine Barrens the point fire frequency may have ranged between 6 to 18 years, with a likely average frequency of once every 10 years (Givnish et al. 1988). Thus, these communities were composed of a constantly changing patchwork of habitats, reflecting the hit or miss nature of recent wildfires. Interdispersed through this patchwork were the recently disturbed sites supporting Karner Blue populations.

Unfortunately, our society tends to abhor wildfire because of the perceived destructive nature of fire. Thus, oak barrens/savanna ecosystems adjacent to urbanized areas are subject to routine/reflexive fire suppression and state and national forests routinely suppress wildfires on their lands. With few positive attributes to associate with wildfire, active ecosystem management still remains controversial to the general public in many areas. Thus, society generally deprives these ecosystems of the very force that created them, a predictable and frequent fire disturbance regime.

Urban and agricultural encroachment, in addition habitat elimination, fragment barrens/savanna communities by inserting non- or less-flammable land uses into a highly

flammable ecosystem (Givnish et al. 1988). These barriers limit the occasional wildfire to small land tracts, reducing the potential for naturally spreading wildfire to maintain the ecosystem in an early successional state. In addition, urban encroachment increases the difficulty of using controlled burns to manage oak barrens/savanna communities because of the liability and perceived danger/nuisance to residents.

Without the influence of a disturbance regime, oak barrens/savanna communities have succumbed to other community types. The impact of fire suppression on these communities has been as great or greater than outright habitat destruction in most areas. For example, oak barrens are critically endangered and the Karner Blue is extirpated from Ohio's Oak Openings, despite the "preservation" of over 9000 acres by state, local and private organizations. Most of the habitats in the Oak Openings which once may have supported oak barrens/savanna have converted to young oak forest. Similarly, what remains of the Albany Pine Barrens in New York has converted into a largely overgrown ecosystem (Givnish et al. 1988). At its worst, land is dominated by black locust forests; at its best, dense scrub oak brushland is dominant.

Disruption of metapopulation dynamics. The plants and animals that together form oak barrens/savanna communities are adapted to the ecosystem level processes which originally structured these communities. To persist regionally in this dynamic ecosystem type, invertebrates must cope with both the ecosystem patch dynamics as well as the forces driving patch dynamics. In simple terms, invertebrates populations must shift locations as quality habitats become available/unavailable and they must be able to survive wildfire, either directly or indirectly. While healthy metapopulations of the Karner Blue may seem to occupy entire barrens/savanna ecosystems, individual sub-populations are usually highly localized and isolated from neighboring populations by barriers of unsuitable habitat. These isolated sub-populations are vulnerable to extinction from both community succession and ecosystem disturbance regimes.

Unfortunately, the Karner Blue is not well adapted to survive fire directly (e.g., Iftner et al. 1992, Swengel 1994). The very mechanism critical for creating and maintaining habitat for this species, fire, also kills all life stages of the butterfly (although there is emerging evidence that the Karner Blue may occasionally survive cool, low fuel-load fires, but requires better documentation). Recently burned habitats must be colonized or recolonized by individuals immigrating from nearby or adjacent habitats. Confounding this is the limited dispersal abilities of the adults. Givnish et al. (1988) estimate that maximum dispersal distance for colonization of unoccupied habitats is approximately 0.5 miles. This agrees closely with values obtain in North Wales for the ecologically similar and related butterfly, *Plebejus argus* in North Wales (Thomas & Harrison 1992): i.e., metapopulation dynamics of *P. argus* over a seven year period indicated that the likelihood of colonizing suitable habitats decreased rapidly in habitats more than 1 km away from potential source populations. These authors concluded that if the continuity of suitable habitat distribution was broken within an ecosystem, entire metapopulations of *P. argus* were likely to collapse.

Because most oak barrens/savanna communities are suffering from the effects of fire suppression, optimal Karner Blue habitats are generally limited in size and widely dispersed. This combination of reduced optimal habitat patch size combined with increased distance between optimal habitat patches has disrupted the metapopulation dynamics of the Karner Blue. For example, suitable but unoccupied habitats may not have a nearby Karner Blue source population from which colonization is possible. Likewise, occupied habitats may require recolonization following fires; recolonization has become less likely as the distance separating occupied habitats increases. In effect, the rate of localized population extinction has been accelerated by declining habitat suitability and size, while the odds of new colonization events have declined as optimal habitats become increasingly fragmented due to succession and alteration. This disruption of metapopulation dynamics is currently causing the downward spiral of several metapopulations of the Karner Blue, even as regional attempts to restore these ecosystems proceed.

The dance with fire. For the Karner Blue, the interplay between habitat suitability, habitat distribution and patch dynamics, metapopulation dynamics and metapopulation persistence is complex. This is best illustrated by the historical distribution of the butterfly itself. The ecosystems known to support metapopulations of this butterfly are generally

large, measured in tens of thousands of acres. Smaller sand barren/oak savanna complexes are less likely to have supported Karner Blues in historic times. This is probably a reflection chance interplays between ecosystem processes and metapopulation dynamics: the larger the ecosystem, the better the odds that all the pieces fall together and populations persist. Smaller ecosystems may have provided fewer opportunities for population persistence, and Karner Blue populations did not persist to historic times. As Givnish et al. (1988) poetically state, persistent populations exist as a "flickering mosaic of Karner Blue populations, with some going extinct in a given area as others are being founded on sites recently burnt by colonists from sites burnt a somewhat longer time ago." In smaller ecosystems, these populations may simply flicker out.

However, given that almost every oak barrens/savanna community in the Midwest must now be actively managed to persist, much of the element of chance can be removed from Karner Blue management. With intensive management, which includes carefully planned burn units to create suitable habitats, Karner Blue populations should be manageable on preserves as small as 200 acres. At this scale, management would have to be almost mechanical, with approximately 10–15% of the entire land-base burned annually, and the burn units configured to provide adequate dispersal opportunities for Karner Blues. Larger areas could be managed less mechanically, but would still require carefully planned management activities. Small management units could be used to establish core populations within larger ecosystem management areas, from which dispersing butterflies could become more widely established.

Finally, to protect against catastrophic disaster, several independent sets of Karner Blue populations should be maintained in each oak barrens/savanna ecosystem. Because of the flammable nature of the ecosystems, true wildfires that consume thousands of acres at one time are a reality. Because individual Karner Blue populations may succumb to such an event, independent core populations should be dispersed through the ecosystem to ensure that single catastrophic events cannot eliminate entire metapopulations.

Preserve managers and stewards must struggle to re-establish the processes that created the barrens and savanna ecosystems they manage. If the Karner Blue is to survive, we must literally take it back to the big dance, where metapopulations swirled with patch dynamics to the music of fire. By managing remnant barrens and savanna communities in light of large-scale ecosystems processes, it should be possible to preserve not only the Karner Blue, but the untold other inconspicuous life-forms adapted to these ever changing ecosystems.

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LIFE HISTORY NOTES FOR THE PALLID EMPEROR MOTH, *CIRINA FORDA* (SATURNIIDAE) IN NIGERIA

Additional key words: phenology, hostplants, Africa.

Cirina forda Westwood has long been known as a serious pest of the sheanut tree, *Vitellaria paradoxa* (Sapotaceae) in Nigeria (Golding 1929). Packard (1914) described the larva, and Boorman (1970) and Leleup and Beams (1969) provided brief accounts of the biology and phenology of this moth. Leleup and Deams (1969) reported *Erythropheum africanum* as a larval host in northern Zaire, but that the tree does not occur in Nigeria. The dried larvae of *C. forda* are referred to locally as “manimani,” and are of economic

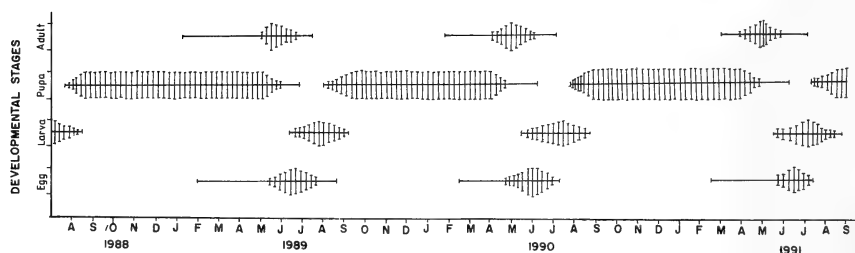
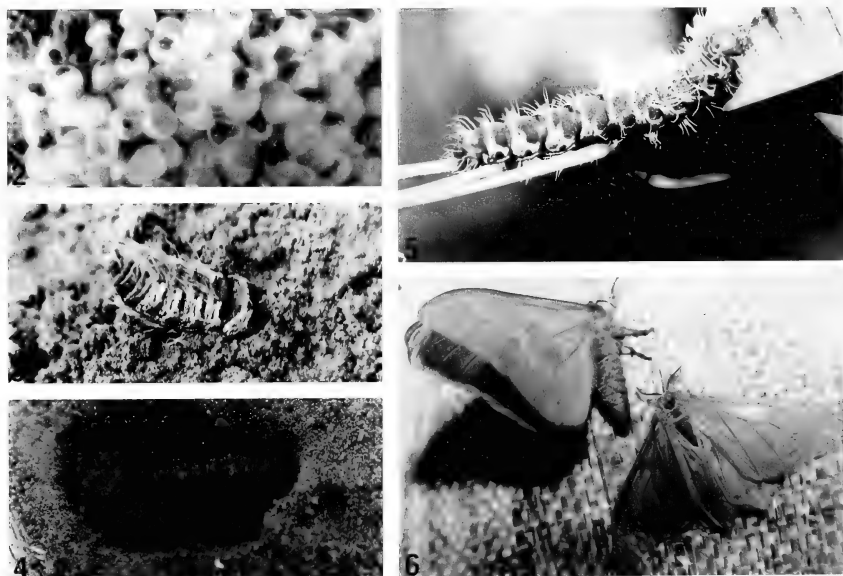


FIG. 1. Phenology of *Cirina forda* in Nigeria, 1988–1991.

importance as a food item among the Nupe tribe of Nigeria. For many decades, wild larvae have been collected, dried and sold to neighboring states within and outside the country, and the insect is considered a delicacy (Ande 1991, Fasoranti & Ajiboye 1993). We report here on the life history and biology of *C. forda* in Nigeria, and its association with *Vittalaria paradoxa*.

About 900 late instar *C. forda* were collected from *V. paradoxa* plants in August 1988, between km 107 and 108 on the Mokwa-Bida road in Niger State, Nigeria (9°05'N, 5°59'E). Subsequently, rearings were conducted in the laboratory at the University of Ilorin between 1989 and 1991. Egg clusters laid in the laboratory were observed daily for hatching. Larvae from the same egg clutch were reared separately on cut and potted twigs of *V. paradoxa* and again on *V. paradoxa* plants outside in an ornamental garden. Twigs were replaced as necessary to maintain freshness, and larvae were transferred carefully by hand and placed on the mid rib or leaf margin of new foliage. A wooden cage (30 cm × 30 cm × 50 cm) with ten compartments was filled to a depth of 20 cm with soil. Ten larvae were then placed in each compartment. As soon as pupation began, the soil was in all compartments examined for pre-pupae and pupae. Pre-pupa duration was defined as the pe-



FIGS. 2–6. 2, egg cluster. 3, pre-pupa. 4, fully formed pupa. 5, late instar. 6, adults (female above, male below).

riod between soil penetration and actual pupation (in days). Subsequently, 30 pre-pupae were randomly selected and placed individually in soil 10 cm deep, each in cylindrical paper eclosion chambers (8 cm diam \times 15 cm deep \times 2 cm thick). The open end of the cylinder was covered with a nylon mesh secured by a rubber band. Each compartment was examined daily for emerging adults. Pupal duration was calculated as the mean number of days between pupal formation and date of adult emergence. Notes were also kept on adult longevity.

Fig. 1 shows the phenology of *C. forda* for the period between 1988 and 1991. Adult moths lived for between 36 and 48 hours (mean = 39.7) and were found primarily in May, with peak oviposition at the end of the month. Figs. 2–6 show the immature stages of *C. forda*. The egg (Fig. 2) hatches after an incubation period of 30 to 34 days (mean = 31.8) into an active and voraciously feeding larva, and passes through 5 to 6 instars (Fig. 5) in 42 to 50 days (mean = 47.5) between June and August. By the first few days in August, most of the larvae reach the pre-pupal stage (Fig. 3) and burrow into the soil. The pre-pupa develops into a pupa (Fig. 4) in 6–7 days and remains in diapause for 9 months (261 to 296 days, mean = 267.5). Adult moths (Fig. 6) emerge in May of the following year.

The life cycle of *C. forda* is tightly linked to the biology of its host, *Vittellaria paradoxa*. The only savannah species of the family Sapotaceae in Nigeria, *V. paradoxa* blossoms fully between May and August when mature fruits become available, and sheds leaves between November and February (Kaay et al. 1964). May and August is when the majority of *C. forda* larvae are developing in the field, and pupation takes place during the dry months of November and April. *C. forda* is univoltine in Nigeria and the phenology reported here agrees with those given by Golding (1929) and Boorman (1978). However, Leleup and Deams (1969) indicate that the active period for *C. forda* in Zaire is between June and September during dry months. In Nigeria, the active periods occur during the wet months of May and August.

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SUPPLEMENT TO THE LIST OF THE BUTTERFLIES OF MICHIGAN

Additional key words: HesperIIDae, LycaenIDae, NymphalIDae, faunal surveys, checklists.

The following contribution represents an addition to the previously published faunal lists for Michigan Lepidoptera (Moore 1960, Perkins 1968, Nielsen 1970). Records range from 1941 to the present time, and represent collecting by myself. Two state zones (NLP = Northern Lower Peninsula; SLP = Southern Lower Peninsula) are recognized, and county names are given for individual records. A date with a trailing asterisk represents the earliest date captured whereas a leading asterisk represents the latest date of capture in a zone. Nomenclature follows Hodges (1983).

Erynnis icelus (Scudder & Burgess) (HesperIIDae) SLP: Barry; *June 26
Erynnis horatius (Scudder & Burgess) (HesperIIDae) SLP: Oakland
Cartocephalus palaemon mandan (Edwards) (HesperIIDae) SLP: Oakland; June 20*
Thymelicus lineola (Ochsenheimer) (HesperIIDae) NLP: Newaygo. SLP: Huron
Hesperia sassacus Harris (HesperIIDae) SLP: Barry
Polites coras (Cramer) (HesperIIDae) SLP: Barry
Wallengrenia egeremet (Scudder) (HesperIIDae) NLP: Newaygo
Pompeius verna (Edwards) (HesperIIDae) SLP: *19 August
Poanes hobomok (Harris) (HesperIIDae) SLP: Barry; *July 11
Euphyes bimacula (Grote & Robinson) (HesperIIDae) NLP: Newaygo; *July 15
Euphyes ruricola metacomet (Harris) (HesperIIDae) SLP: *August 19
Papilio polyxenes asterius Stoll (PapilionIDae) SLP: Huron
Papilio troilus Linnaeus (PapilionIDae) NLP: Newaygo
Artogeia rapae (Linnaeus) (PierIDae) SLP: Lapeer, Sanilac, Tuscola
Colias philodice Godart (PierIDae) NLP: Newaygo. SLP: Sanilac, Tuscola; May 4*
Colias eurytheme Boisduval (PierIDae) SLP: Huron, Lapeer, Sanilac, Tuscola
Lycaena phlaeas americana Harris (LycaenIDae) NLP: Newaygo. SLP: *October 1
Hyllolycaena hyllus (Cramer) (LycaenIDae) SLP: Tuscola
Epidemia dorcas (Kirby) (LycaenIDae) SLP: June 13, *August 19
Epidemia helleoides (Boisduval) (LycaenIDae) NLP: Newaygo
Harkenclenus titus (Fabricius) (LycaenIDae) NLP: Newaygo
Satyrium edwardsii (Grote & Robinson) (LycaenIDae) SLP: *5 August
Satyrium caryaevorum (McDunnough) (LycaenIDae) SLP: June 26*
Satyrium liparops strigosum (Harris) (LycaenIDae) SLP: *August 19
Everes comyntas (Godart) (LycaenIDae) NLP: Newaygo. SLP: Huron
Celastrina ladon (Cramer) (LycaenIDae) NLP: Newaygo
Aglaia milberti (Godart) (NymphalIDae) SLP: Barry
Vanessa virginianensis (Drury) (NymphalIDae) SLP: Barry
Vanessa cardui (Linnaeus) (NymphalIDae) SLP: Huron
Phyciodes tharos (Drury) (NymphalIDae) SLP: Lapeer; *Oct 1
Euphydryas phaeton (Drury) (NymphalIDae) SLP: *August 7
Basilarchia archippus (Cramer) (NymphalIDae) SLP: Tuscola
Cercyonis pegala nephele (Kirby) (Satyridae) SLP: July 3*

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REDISCOVERY OF *LETHE EUROPA TAMUNA* WITH NOTES ON OTHER THREATENED BUTTERFLIES FROM THE ANDAMAN AND NICOBAR ISLANDS

Additional key words: Legal protection, status reassessment.

Drawing on data from the IUCN Conservation Monitoring Centre, the United Nations Environment Program (UNEP) (1987) listed six species of butterflies as threatened from the Indian coastal region. Four of these—one species and three subspecies—are endemic to the Andaman and Nicobar islands (Table 1). Three of these taxa have been termed “very rare” while *Graphium epaminondas* Oberthur was termed “locally common” by both Evans (1932) and Ferrar (1948). Khatri (1996) recently reported that two of these taxa, *Lethe europa tamuna* de Niceville and *Neptis sankara nar* de Niceville, were extirpated on these islands. We present here new information on three of the four taxa rated “threatened” from the Andaman and Nicobar islands, including biological notes on the rediscovery of *Lethe europa tamuna*.

Lethe europa tamuna de Niceville (Nymphalidae: Satyrinae). This is one of the rarest butterflies from the islands, being known previously from a single female specimen collected on Little Nicobar. Ferrar (1948) reported observing another female on Great Nicobar some time before he left the islands in 1931. On a collecting trip to Great Nicobar Island in December 1996, the senior author observed four females, and found two eggs and two larvae of this butterfly at three localities in the Campbell Bay area of Great Nicobar. Both the adults and immatures were found along roadsides where the forests had been disturbed by human activity. One of the females was seen resting on moist sand on the banks of a stream. Another female was observed ovipositing on the upper surface of a leaf of the climbing bamboo, *Dinorchloa andamanica* Kurz. Eggs were laid on leaves well within the clump, not on the fringes. The larvae (Fig. 1B) were sleeved and observed periodically for about two weeks. They fed and passed through several instars, and confirmed *D. andamanica* as a host plant that supports development. We suspect this butterfly is not as rare as previously thought, but its status can be reliably assessed only after further studies are conducted.

Doleschallia bisaltide andamana Fruhstorfer (Nymphalidae: Nymphalinae). This butterfly has been considered rarer in the Nicobars (Car and Central Nicobar) than in the Andaman islands (Evans 1932, Ferrar 1948). Its cryptic habits have perhaps contributed to an underestimate of its abundance. We have observed eggs, larvae and adults of this butterfly at S. Andaman and at Great Nicobar. The larvae completed their life cycles on the plants on which they were found, when sleeved (see Table 1). We found from 15 to 58 adults feeding on the small white blossoms of medium sized trees of *Ligustrum glomeratum* Blume (Oleaceae) at Chidyatapu (Fig. 1D) in S. Andaman in 1994, 1995 and 1996. At Campbell Bay on Great Nicobar, 16 eggs were observed on *P. album* (Nees) Merr. (located in less than 30 min of search); 3 females were also observed in flight.

TABLE 1. Threatened species of butterflies for the South Asian Seas region from the data base of the IUCN Conservation Monitoring Centre (UNEP 1987). Status represents ratings by Evans (1932) and Ferrar (1948); IUCN categories are as defined prior to Mace & Lande (1991) and Mace & Stuart (1994). All except *Graphium epaminondas* are listed as Schedule I species in the Indian Wildlife (Protection) Act, 1972 as revised to 1991.

Taxon	Region	Distribution	Status	IUCN Category	Larval Foodplant
<i>Lethe europa tamuna</i>	India	S. Nicobars	very rare	rare	<i>Dinochloa andamanica</i> Kurz (Poaceae)
<i>Doleschallia bisaltide andamana</i>	S. Asia	Andamans	not rare	rare	<i>Pseuderanthemum album</i> (Nees) Merr. (Acanthaceae)
		Car Nicobars	very rare		<i>Phaulopsis imbricata</i> (Forst.) Sweet (Acanthaceae)
		Central Nicobars	very rare		
<i>Neptis sankara nar</i>	India	N. Andaman	very rare	rare	unknown
<i>Graphium epaminondas</i>	S. Asia	Andamans	not rare, locally common	insufficiently known	<i>Uvaria rufa</i> Bl. (Annonaceae)

Graphium epaminondas Oberthur (Papilionidae: Papilioninae). Although this butterfly was among the first collected from the islands (Hewitson 1874), nothing was known about its biology until its larval host plant and life cycle were worked out (Prashanth Mohanraj & Veenakumari 1994). It has a very short flight period with adults on the wing between April and June (Prashanth Mohanraj & Veenakumari 1996). It is localized in its distribution on S. Andaman. Mount Harriet National Park and some other localities on S. Andaman continue to support good populations of the butterfly, but we consider it has declined in abundance from the earlier reports by Evans (1932) and Ferrar (1948). The species is not currently threatened though some of its breeding localities have been destroyed (Prashanth Mohanraj & Veenakumari 1996).

Neptis sankara nar de Niceville (Nymphalidae: Nymphalinae). About half a dozen historical specimens of this species have been collected from the Andaman islands (Ferrar 1948). No specimens have been collected recently, and we have not encountered the species in our studies. If the butterfly is confined to N. Andaman (where Ferrar spotted his only specimen) then we may well have missed this species on our short, sporadic visits to the island. We doubt the species is extirpated, as N. Andaman is far less disturbed than S. Andaman.

Over one fourth of the butterflies of the Andaman and Nicobar islands have been rated as "rare" or "very rare" by Ferrar (1948), the only person to have collected diligently for as long a period as eight years from these islands. Given the relative paucity of data, we feel that until more detailed field studies on Andaman and Nicobar butterflies are conducted, statements about the status of the islands' species should be made with caution.

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FIG. 1. Lepidoptera from Andaman and Nicobar Islands: A, adult *Lethe europa tamuna*; B, larva of *Lethe europa tamuna*; C, the strikingly different larva of *Lethe europa nudgara* (ssp. *tamuna* is confined to the S. Nicobars while ssp. *nudgara* is restricted to the Andamans); D, *Doleschallia bisaltide andamana* feeding on a blossom of *Ligustrum glomeratum* Blume.

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CORRECTION TO VOLUME 51

In the article by Annette Aiello and Manuel A. Balcazar L., "The immature stages of *Oxytenis modestia*, with comments on the larvae of *Asthenidia* and *Homoeopteryx* (Saturniidae: Oxyteninae) which appeared in 51(2):105–118, the caption for Figure 1 contains an error. It should read Lot 85-126, not Lot 85-26.

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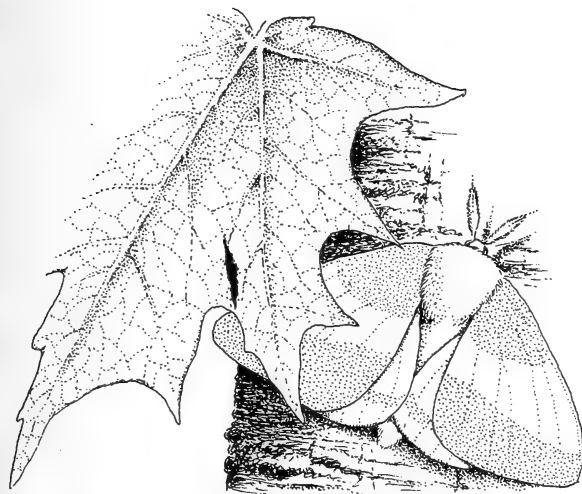
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Cover illustration: the Rosy Maple moth, *Dryocampa rubicunda* Fabr., a common saturniid found in eastern North America. Original pen and ink drawing by John Himmelman, 67 Schnoor Road, Killingworth, Connecticut, 06419, USA.

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INTOXICATED LEPIDOPTERANS: HOW IS THEIR FITNESS AFFECTED, AND WHY DO THEY TIPPLE?

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ABSTRACT. Butterflies imbibing fluids at fallen, rotting fruits sometimes show signs of intoxication. Fallen fruits as well as woody plant sap-flows undergo natural fermentation, which may result in frothy brews containing up to perhaps 3% ethanol. Many lepidopterans are attracted to volatile fermentation products, but studies of actual consumption are lacking. In laboratory choice tests, adults of *Choristoneura fumiferana* (Clemens) neither favored nor shunned 1% ethanol in plain or sweetened water for imbibing. Adults imbibing up to 1% ethanol were unimpaired in six of seven monitored fitness factors. One fitness factor, fertility, defined as the proportion of pairs reproducing, declined incrementally starting at concentrations of 0.5% ethanol. Two hypotheses are presented to explain lepidopteran intoxication in nature.

Additional key words: *Choristoneura fumiferana*, Tortricidae, imbibing, fermentation, ethanol.

Butterflies may become sluggish and more easily captured while imbibing fluids at fallen, rotting fruits, and collectors often use fermenting brews as baits (Norris 1936, Utrio & Eriksson 1977). Because the sweet fluids of fallen fruits and woody plant sap-flows may ferment (Janzen 1977), it is assumed that lepidopterans imbibing them become intoxicated from fermentation products such as ethanol. Although the attractancy of fermentation products to certain lepidopterans has been experimentally documented (Utrio & Eriksson 1977, Utrio 1983), studies of actual ferment consumption are lacking. Neither lepidopterans nor other insects are among the invertebrates featured in Winterstein's (1919) classic treatise on narcosis.

Unlike butterfly intoxication, moth intoxication does not seem to have been reported despite the fact that most of the experimental work on ferment attractancy utilized moths. Moths typically feed at dusk or after dark, times when they are difficult to observe in the wild. Also, in the era before sex lures, attractancy research was done to support prescriptions for trapping and monitoring lepidopteran pests in fruit orchards

(Dethier 1947, Green et al. 1960, Madsen & Morgan 1970), a context in which consumption and intoxication were irrelevant. Species in four moth families have nevertheless been recorded at natural sap flows, namely Noctuidae, Sphingidae, Geometridae, and Tortricidae (Norris 1936, Foster & Tate 1966).

Fermentation is the chemical alteration of carbohydrates by microorganisms. The microorganisms involved are usually yeast fungi and their close relatives, of which more than 500 species in 54 genera are recognized (Phaff et al. 1978). Different yeasts give rise to different fermentation products, and naturally produced ethanol is thought to be fairly common. It is not unusual for imbibed ferments to be described as frothy (Wilson 1926, Foster & Tate 1966, Simon & Enders 1978). Frothiness results from the co-production of carbon dioxide with ethanol (Phaff et al. 1978). Yeasts are believed to be introduced by insects to fallen fruits and woody plant sap-flows (do Carmo-Sousa 1969, Phaff et al. 1978). Woody plant sap-flows result from wounding by a variety of biotic and physical agents, as well as from unknown causes (Wilson 1926, Ohman & Kessler 1964, Simon & Enders 1966, Radwan 1969).

Here I examine whether or not individual *C. fumiferana* adults in the laboratory prefer diets for imbibing that contain 1% ethanol. I also compare the following seven fitness factors between groups of adults receiving diets spiked with concentrations of 0.1–5% ethanol: fertility, lifespan, preoviposition period, oviposition period, time to 80% oviposition, fecundity, and egg hatch. In designing and conducting this study, I drew heavily on previous personal experience with adult feeding in *C. fumiferana* (Miller 1987, 1989).

MATERIALS AND METHODS

The adults used here were collected as pupae from balsam fir (*Abies balsamea* [L.] Mill.) and white spruce (*Picea glauca* [Moench] Voss) in two successive years at three sites within 6 km of Hovland, Cook Co., Minnesota. The pupae were sexed using the guide of Jennings and Houseweart (1978). Sexed pupae were placed one pair per container in 1-pint (0.48 l) round cardboard ice cream cartons whose bottoms and tops were replaced with Petri dish bases and lids. Male and female pupae were matched developmentally so as to maximize eclosion synchrony. Pairs were assigned sequentially to different ethanol concentration treatments within fitness experiments so that early and late eclosing pairs would be equally distributed throughout. A fresh sprig of balsam fir 5–8 cm long was placed in each pair container as an oviposition substrate. Containers were kept on a table in a laboratory maintained at 25°C on a 12L:12D fluorescent lighting schedule. Diets for imbibing were provided to moths by means of saturated 3–4 cc³ synthetic

sponges. In the fitness experiments, there was one sponge per container, and the diet was renewed at intervals of 1–2 days. In the choice experiment, diets were provided only during tests.

The choice experiment consisted of placing adults individually in a round 1-gallon (3.8 l) 17.5 cm diameter cardboard ice cream carton with a glass cover, and observing each one for 20 min. Moth placement was at the center of the arena floor, 8 cm equidistant from two sponges on opposite sides of the floor, one soaked in a 1% solution of ethanol in either plain or sweetened water, the other soaked in the nonalcoholic equivalent. Sweetened water was 10% honey (v/v). If imbibing occurred, the time to its start was recorded. Each moth of each pair assigned to the choice experiment was used once daily in a test near midday under regular laboratory lighting.

In the fitness experiment with water-based diet, five concentrations of ethanol (0–5%) were provided, and in the experiment with 10% honey, three concentrations (0–1%) (v/v) were provided. In both experiments, data were collected from pair containers once daily near midday. Records were made of female and male eclosion dates, number of eggs laid daily, and dates of male and female deaths. Foliage was inspected for eggs with a 9 cm diameter reading glass. Eggs were removed from moth containers daily, counted under a stereomicroscope, and placed in labeled Petri dishes. Egg dishes were checked once daily to count the numbers of eggs hatching. Pairs were deemed fertile if the female laid any viable eggs. At death, females were stored in a freezer until they could be dissected for counting unlaidd mature eggs. Size and low stainability with methylene blue were the criteria by which unlaidd eggs were deemed chorionated and thus mature or ripe (Miller 1987).

RESULTS

Diet-choice experiment. Thirteen female and 13 male adults were observed 92 times in the choice arena. Because choice results with plain and sweetened water diets were virtually identical, they were pooled. The pooled results show that no choice was made 43 out of 92 times, an outcome consistent with previous findings that the moths do not always imbibe when given the opportunity (Miller 1989). Among the 49 choices made, the chosen diet was as often nonalcoholic as alcoholic (Fig. 1). Adults choosing the nonalcoholic diet took 5.5 min (SD = 6.1 min) on average to make a choice, while those choosing the alcoholic diet took 5.4 min (SD = 5.7 min). The moths that promptly made a choice walked directly to the sponge, often turning around once in place first. The preponderance of females over males in Fig. 1 is due to longer female lifespans.

Fitness experiments. Moths receiving 5% ethanol became ex-

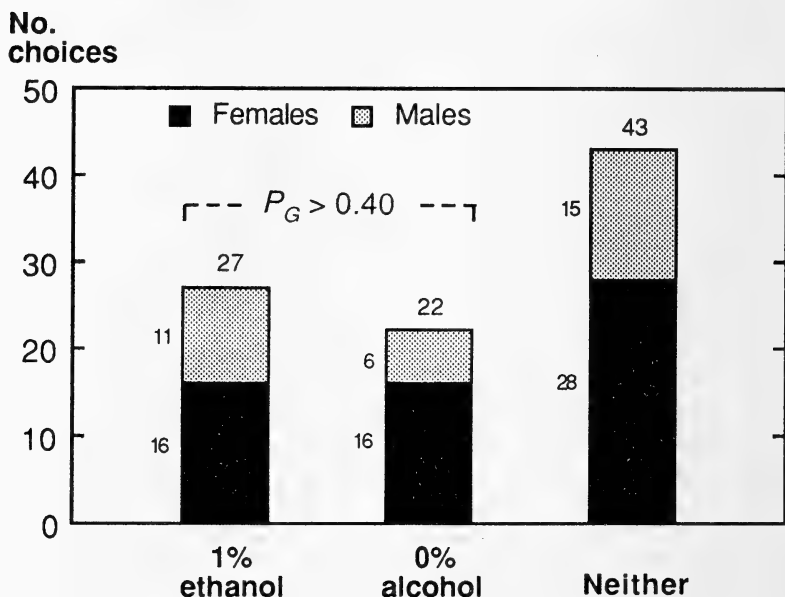


FIG. 1. Diet choices made within 20 min by individual *Choristoneura fumiferana* adults placed in the center of a 1-gallon (3.8 l) container with alcoholic and nonalcoholic diet sponges on opposite sides of the 17.5 cm diameter bottom. The alcoholic diet was 1% ethanol in either plain water or 10% honey water, and the nonalcoholic diet the same without ethanol. Results for the two experiments with different diet bases are pooled. The frequencies were tested for independence in a 2×2 contingency table using the G statistic.

tremely intoxicated. They were lying on their backs within minutes after imbibing. Fourteen out of 16 did not reproduce, and although these remained alive for a few days, they always appeared comatose. At 1% ethanol, no signs of intoxication were evident.

Fertility results from the two fitness experiments were pooled because of similar reproductive fractions in each experiment (Table 1). Fertility is broadly defined as the proportion of pairs reproducing (reproductive fraction). Pooled fertility dropped from 67% to 12% on diets of 0% to 5% ethanol, respectively (Fig. 2). Fertility of 67% at 0% ethanol is typical of normal laboratory fertility of *C. fumiferana* (Outram 1971, Miller 1987, 1989). Distinct fertility reduction started at 0.5% ethanol.

Results other than fertility from the two fitness experiments were not pooled because of the underlying differential effects of plain and sweetened water (Table 1; also Miller 1987, 1989). Within each experiment, preoviposition period, oviposition period, time to 80% oviposition, and lifespans of the sexes did not differ significantly among ethanol concentrations 0–1% (Table 1). It must be emphasized that these results represent only the fertile pairs at each ethanol concentration; results based on

TABLE 1. Performance of reproducing moth pairs receiving diets with different ethanol concentrations. Means are followed by SD's in parentheses. Only reproductive fractions pooled from the two experiments differ significantly among ethanol concentrations (Fig. 4); differences in other factors among ethanol concentrations of 0–1% are not significant ($P_F > 0.20$). Results for 5% ethanol were not included in the statistical analysis because of the small reproductive fraction.

Factor	Ethanol concentration				
	0%	0.1%	0.5%	1%	5%
Water-based diet					
Reproductive fraction, pairs/pairs	12/16	11/17	10/16	10/17	2/16
Mean preoviposition period (days)	2.8 (0.8)	2.3 (0.7)	2.8 (1.1)	3.1 (1.8)	1.0 (0.0)
Mean oviposition period (days)	7.4 (2.2)	5.0 (2.2)	5.0 (2.9)	5.1 (3.1)	3.5 (0.7)
Mean period female emergence to 80% oviposition (days)	7.2 (1.7)	6.0 (1.6)	6.3 (1.9)	6.6 (2.2)	4.5 (0.0)
Mean lifespan (days)					
female	10.2 (1.9)	7.2 (2.4)	7.8 (2.5)	7.8 (2.8)	4.5 (0.7)
male	8.7 (2.5)	7.0 (2.3)	8.1 (1.8)	6.7 (1.6)	5.5 (2.1)
10% honey-based diet					
Reproductive fraction, pairs/pairs	12/20	—	8/21	6/21	—
Mean preoviposition period (days)	2.2 (0.6)	—	2.2 (0.9)	2.5 (1.0)	—
Mean oviposition period (days)	13.6 (3.4)	—	14.1 (6.5)	17.3 (3.6)	—
Mean period female emergence to 80% oviposition (days)	9.2 (1.9)	—	8.8 (3.4)	9.8 (1.7)	—
Mean lifespan (days)					
female	15.8 (3.2)	—	16.4 (6.6)	19.8 (3.1)	—
male	12.4 (4.1)	—	10.5 (4.9)	11.3 (6.2)	—

all pairs would differ moderately among ethanol concentrations. It is clear without statistical analysis that the two reproducing pairs receiving 5% ethanol (Table 1) were severely impaired. These moths may have survived because of weak imbibing tendencies.

Numbers of eggs produced, laid, and hatched showed no significant differences among concentrations of 0–1% ethanol (Figs. 3, 4). Here again, the two pairs that reproduced on 5% ethanol clearly underperformed (Fig. 3). The absence of increase in fecundity of females on alcoholic compared with the nonalcoholic diets suggests that alcohol was not metabolized for energy.

DISCUSSION

Technically, "intoxication" refers to behavior while "toxication" refers to deeper effects such as fitness. Throughout this paper I use the more familiar term to refer to both. Gomez's (1973) description of intoxication in a female *Opsiphanes cassiae* L. (Nymphalidae), quoted below, appears to be the most detailed for a butterfly. The butterfly accidentally flew indoors and alighted near an uncorked bottle of wine containing

Percent pairs reproducing

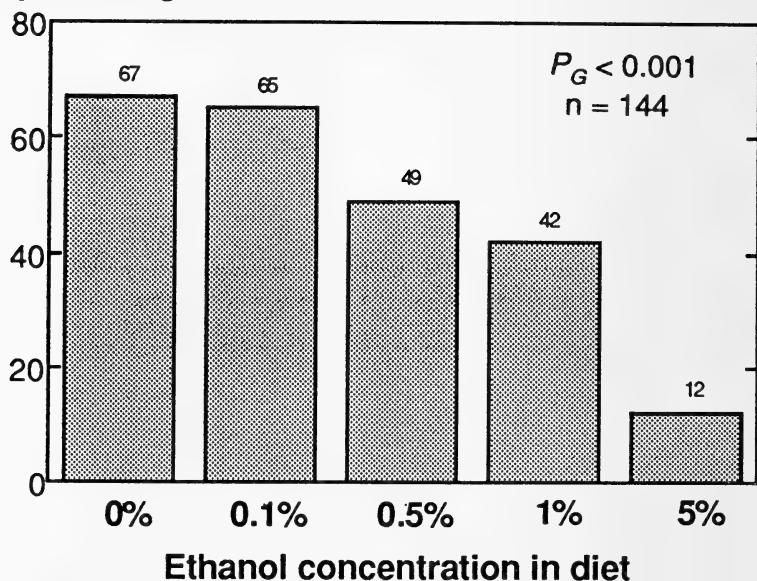


FIG. 2. Fertility or reproductive fraction of pairs of *Choristoneura fumiferana* adults receiving different ethanol concentrations for imbibing. Results for the two experiments with different diet bases are pooled.

12% ethanol. Imbibing a drop of proffered wine, it began to act abnormally within 5 min.

"First, some very slow up and down flapping of wings, followed by forewings being lowered and directed forward with brisk movements several times, hindwings remaining upright . . . [and moving] forward . . . until . . . propped far ahead of their normal resting position. Antennae were lowered until they touched the table. . . . Movement of fore-, hindwings and antennae were repeated several times. . . . After a brief period of inactivity, a hopping spastic side-walking took place alternating with wing and antennae motions as well as a tremulous and agitated moving of the legs. More wine was offered to the insect which sipped it directly from my fingertip. . . . Another sequence of the behaviour described above was observed until all wings were placed flat on the table. . . . A few forward strokes of forewings followed by a very fast vibratory flapping preceded a period of inaction. A few minutes later the butterfly took flight in a close-spiralling pattern towards an incandescent light, hitting the hot bulb several times, alighting and again attempting flight to the light . . . close to which it finally perched. After a few hours it resumed normal behaviour and flew away the next day."

Where adults are short lived, as in *Choristoneura fumiferana*, intoxication is more appropriately viewed in a fitness than behavioral context because reproduction is the predominant activity. The most ethanol-sensitive fitness factor proved to be fertility, broadly defined as the proportion of pairs reproducing (reproductive fraction). Fertility declined sharply from 49% at 0.5% ethanol to 12% at 5% ethanol (Fig. 2). It is

Mean no. eggs per female

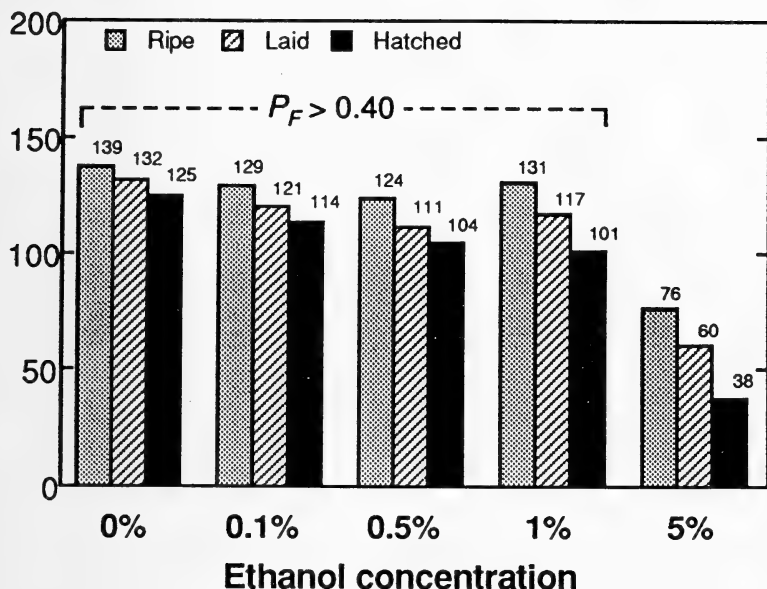


FIG. 3. Fecundity, oviposition, and egg hatch for *Choristoneura fumiferana* pairs receiving different ethanol concentrations in plain water for imbibing. Results represent fertile pairs only. F -tests were done separately for each egg category.

unclear at which interval fertilization was disrupted in the reproductive sequence of assembly, copulation, spermatophore transfer, sperm storage, and sperm use. However, the fact that females, and presumably males, are not known to imbibe until the third day of adulthood (Miller 1989) suggests disruption following spermatophore transfer, an interval usually occurring on the first or second day of adulthood (Outram 1971). Nonfertile females were not dissected for spermatophores.

No effects on *C. fumiferana* fitness were evident at 0.1% ethanol (Table 1, Figs. 2–4). However, it must be noted that actual quantities of ethanol ingested in this study are unknown. Previously, females were found to imbibe a mean of 4.5 mg of fluid per feeding (range of 0.9–10.0 mg) (Miller 1989).

One prominent instigator of sap-flows in forests inhabited by *C. fumiferana* is the yellow-bellied sapsucker, *Sphyrapicus v. varius* (L.). This bird pecks squarish holes through the bark to the sap-conducting phloem in many species of woody dicotyledons and gymnosperms (Foster & Tate 1966). Interiors of the holes are shaped so that sap collects in them. Sapsuckers and many other animals, including lepidopterans,

Mean no. eggs per female

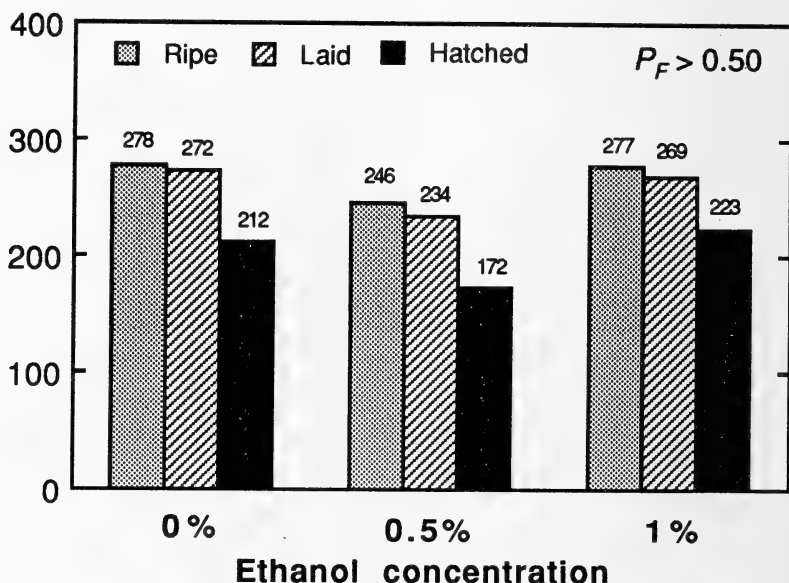


FIG. 4. Fecundity, oviposition, and egg hatch for *Choristoneura fumiferana* pairs receiving different ethanol concentrations in 10% honey for imbibing. Results represent fertile pairs only. *F*-tests were done separately for each egg category.

feed at these reservoirs. Insects that visit them comprise much of the sapsucker diet (Foster & Tate 1966). *Choristoneura fumiferana* adults are also part of the sapsucker diet (Tate 1973), and presumably are among the tortricids at sapsucker feeding holes (Foster & Tate 1966). Intoxication signs sometimes noted in the birds themselves are attributed to ingestion of fermentation products (Pearson 1936, Foster & Tate 1966). Sugar concentration in the sap of feeding holes is typically 1–6%, sometimes higher (Tate 1973). Ethanol concentrations of ferments in nature apparently have not been measured, but typical sugar concentrations in sapsucker feeding holes would yield ethanol concentrations no higher than perhaps 3%, or one-half of the sugar concentration, assuming complete fermentation. However, fermentation may be self-limiting and thus incomplete (Jorgensen & Hansen 1948). Another source of fermentable sugars in forests is aphid honeydews, a food resource adult lepidopterans are also known to exploit (Pittioni 1923, Zoebelein 1956, Johnson & Stafford 1985).

In certain *Drosophila* species, ethanol tolerance and metabolism are well developed and based on specific enzymes. Such species also exten-

sively exploit ethanol as a habitat cue (Chawla et al. 1981, Parsons 1981). By contrast, there is neither evidence for *C. fumiferana* adults metabolizing ethanol for energy, nor evidence for hormesis or small-dose enhancement (Clarke 1990). Whether enzyme-based mechanisms of ethanol tolerance exist in any lepidopteran is unknown.

As to why lepidopterans with imbibing capability tipple in the wild on ethanol or other fermentation products, I offer two hypotheses.

First, lepidopterans that are neither attracted to nor repelled by ferments have life systems that lack the capability to use fermentation products as cues for finding adult feeding opportunities. Tiny amounts of fluids suffice for these small moths to imbibe, and their fitness is increased by water intake with or without dissolved sugars (Norris 1934, Kira et al. 1969, El-Sherif et al. 1979, Miller 1987, 1988). Lepidopterans in this group orient to the water at feeding sites, and intoxication is accidental, *C. fumiferana* being an example.

Second, lepidopterans that are drawn to ferments have life systems with the capability to use fermentation products as cues for finding adult feeding opportunities. Members of this group are large bodied and require ample nutrient fluids containing dissolved sugars and perhaps other ingredients (Portier & de Rorthays 1940, Lukefahr & Martin 1964, Utrio 1983). If these lepidopterans become intoxicated from foraging at ferments, the cost is tolerable given the food value of the unfermented fraction and possibly of the fermented fraction also. *Opsiphanes cassiae*, the intoxicated butterfly described earlier (Gomez 1977), is an example. Other examples include Nymphalidae in the fruit-and-sap-feeding subfamilies Brassolinae, Morphinae, Satyrinae, and Nymphalinae (Young 1979), and many stout-bodied Noctuidae (Utrio 1983). Young (1979) has argued that eye spots on the wings of butterflies that forage at fallen fruits evolved as a defense to offset their greater vulnerability to predation while on the ground, perhaps also while intoxicated.

Future investigations toward understanding lepidopteran intoxication should include more species, more fermentation products, and the composition of ferments at feeding sites.

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HYDROXYDANAIDAL AND THE COURTSHIP OF *HAPLOA* (ARCTIIDAE)

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ABSTRACT. Male *Haploa clymene* display large tubular coremata in the moments before mating. The coremata are deployed in the immediate vicinity of the female's antennae and their eversion is a prerequisite for mating success. The major volatile component associated with the coremata of *H. clymene* and *H. confusa* is the dihydropyrrolizine hydroxydanaidal. In *H. clymene* production of hydroxydanaidal is contingent on larval access to their natural hostplants containing pyrrolizidine alkaloid precursors. The widespread distribution of hydroxydanaidal in arctiid moths suggests a single early evolutionary origin for the ability to produce it. This origin appears to precede the divergence of three arctiid subfamilies: the Arctiinae, Pericopinae, and the Ctenuchinae.

Additional key words: coremata, mating behavior, pyrrolizidine alkaloids.

Male moths of the family Arctiidae possess some of the most morphologically elaborate scent-disseminating structures known in the Lepidoptera (Birch et al. 1990). These structures are most often displayed in the moments before mating and are thought to play a role in sexual selection (Eisner & Meinwald 1995). The pheromonal signals they release have been characterized in several cases, and the compound hydroxydanaidal (or the related compound danaidal) has been identified repeatedly. Hydroxydanaidal is a volatile dihydropyrrolizine (Fig. 1) derived from defensive pyrrolizidine alkaloids (PAs) sequestered from the larval or adult food of each species (Conner et al. 1981, Boppré & Schneider 1985, Krasnoff & Roelofs 1989). We here add *Haploa clymene* (Brown) and *H. confusa* (Lyman) to the growing list of hydroxydanaidal bearers, investigate the dependence of hydroxydanaidal production on larval diet in *H. clymene*, and describe the courtship of this species. We also suggest a single evolutionary origin for hydroxydanaidal production within the Arctiidae.

MATERIALS AND METHODS

Haploa clymene were collected as larvae on *Eupatorium purpureum* L. in Forsyth County, North Carolina. Adults were collected at blacklights and allowed to mate and lay eggs. Larvae were fed fresh leaves of *E. purpureum*, a member of a genus known to contain pyrrolizidine alkaloids (Mattocks 1986), or *Plantago rugelii* Dcne., a plant known to be devoid of pyrrolizidine alkaloids (Cronquist 1981). Additional larvae

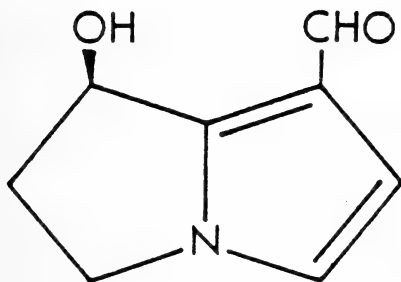


FIG. 1. R-(-)-hydroxydanaidal.

were started on *E. purpureum* for their initial instar and then switched to an alkaloid-free *Manduca* artificial diet (Bell & Joachim 1976) until pupation. All larvae and adults were held at room temperature on a 16L:8D photoperiod regime. Final-instar larvae of *H. confusa* were collected on *Eupatorium maculatum* L. and *Lythrum salicaria* L. by Scott Smedley in Ithaca, New York. These were fed *E. purpureum* until pupation.

Coremata are tubular and inflatable scent-disseminating structures found in males of many species of arctiid moths. They were everted from between the 7th and 8th abdominal segments of 2–4 day old male *Haploa* by gently squeezing their abdomens. The coremata were excised with iridectomy scissors, and dropped into 100 μ l of methylene chloride. Benzophenone was used as an internal standard. Quantitative chromatography was carried out on a Hewlett Packard (HP) 55790A gas liquid chromatograph with an on-column injection port and flame ionization detector. Ultra I (methyl silicone) and Ultra II (phenyl methyl silicone) columns (Hewlett Packard; 25 m, 0.32 mm ID, 0.52 mm film thickness) were used. The carrier flow was 5.0ml/min with an initial temperature of 50°C held for 2 min; the temperature was then increased to 280°C at 5°C/min and held for 2 min. Authentic samples of R-(-)-hydroxydanaidal (99% pure) were provided by Jerrold Meinwald of the Department of Chemistry, Cornell University.

Mass spectrometry and infrared spectroscopy were carried out on an HP 5890 GLC coupled with an HP 5965A infrared detector and an HP 5970 mass selective detector. Compounds were separated on a 60 m, 0.25 mm ID, 0.25 mm methyl silicone column. The initial temperature was held at 100°C for 2 min and increased to 240°C at 2.5°C/min.

Courtship behavior of *H. clymene* was observed and recorded in a laboratory wind tunnel (60 \times 60 \times 150 cm; windspeed = 25 cm/sec) under deep red illumination (<5 lux). Mating sequences were videotaped using a BGC CCD-500E video camera and a JVC BR9000 video recorder.

Ultrasound was monitored using a QMC S200 bat detector and recorded on the audiotrack of the videotape. Some males were rendered incapable of everting their coremata by applying a cyanoacrylate ester-based glue to their partially everted coremata and allowing the coremata to retract.

RESULTS

Haploa clymene mate between 3 h and 7 h after the onset of scotophase. The courtship is initiated by the female through the release of a typical arctiid sex attractant blend. Female pheromone-releasing behavior is readily apparent as the rhythmic exposure of the openings of tubular sex pheromone glands. The sex attractant, composed of Z,Z,Z-3,6,9-heneicosatriene and related compounds (Davidson 1995), stimulates males to fly upwind and seek females. When the male reaches the female he exposes a pair of inflatable cuticular tubes called coremata. They extend from their origin in the intersegmental membrane between the male's seventh and eighth abdominal segments, often encircle the female's abdomen, and curve together just above the head of the female, presumably stimulating her antennae with male courtship pheromone (Fig. 2). Genital contact is made and copulation ensues. Although *Haploa* have well-developed tymbal organs (Fullard & Fenton 1977, Davidson 1995) like those that have been shown to be involved in the courtship of several arctiid species (Simmons & Conner 1996) their courtship is silent.

The major volatile component associated with the coremata of both *H. clymene* (field collected as adults or fed *E. purpureum* through all their larval stages) and *H. confusa* (collected as final instar larvae on *E. maculatum* or *L. salicaria* and fed *E. purpureum* for the remainder of their larval life) matched an authentic sample of hydroxydanaidal in retention time on all three columns, IR spectrum, and mass spectrum (m/z (relative intensity): 151(3.5), 133(59), 104(100), 77(26), 51(35)).

The coremata of male *H. clymene* raised through all larval instars on *E. purpureum* produced an average of 0.88 ± 0.68 μg hydroxydanaidal/individual ($n = 13$) with a range from 0.08 to 2.18 μg /individual. Males raised on *Plantago rugelii* ($n = 1$) or the alkaloid-free diet ($n = 11$) contained no detectable hydroxydanaidal in their coremata (detection limit 0.01 μg /individual). There were no apparent differences in the morphology of the coremata of *H. clymene* raised on the three diets. A composite sample of the coremata of twenty *H. confusa* had a mean coremata titer roughly ten times lower (0.0685 μg /individual).

The courtships of six unoperated male *H. clymene* (reared on *E. purpureum*), each paired with a female, were videotaped in the laboratory wind tunnel. In 5 of 6 cases the coremata of the males were clearly visi-

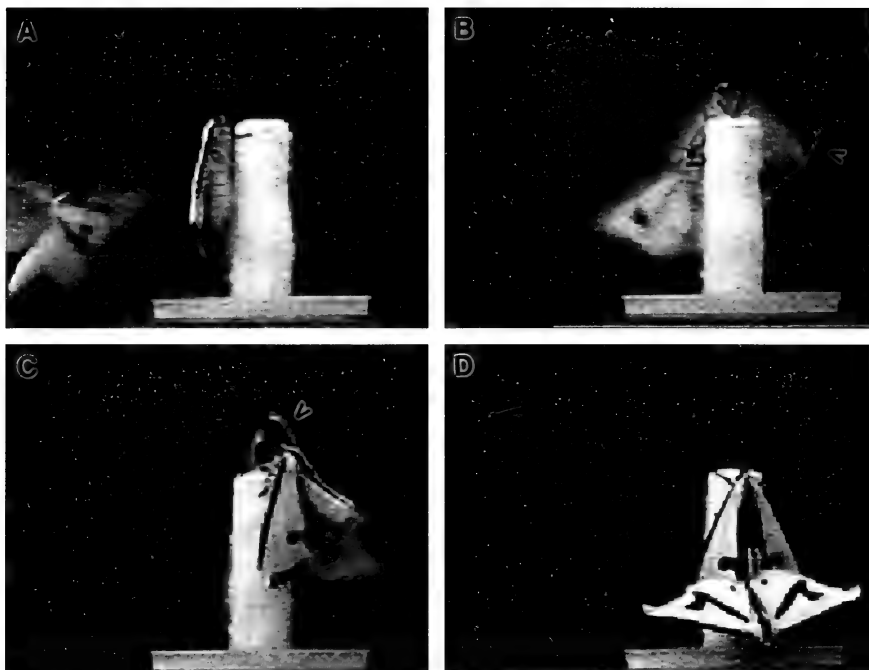


FIG. 2. Freeze-frame video sequence of the courtship of *H. clymene*. A, male approaches female (0.00 sec); B, male everts coremata (1.52 sec); C, coremata reach the antennae of the female (2.24 sec); D, pair in copulo (10.89 sec). Arrows mark everted coremata.

ble and the courtship resulted in copulation. In the one case where the male did not evert his coremata, the courtship was unsuccessful because the female evaded the male by flying away. Three courtship sequences involving males rendered incapable of everting their coremata by gluing were all unsuccessful. In each case the female evaded the male and effectively terminated the encounter. The difference between the success rates of unoperated males and the glued males was significant (Fisher exact probability, $P = 0.047$). Due to the small number of males available sham-operated controls could not be performed for this experiment. However, previous studies indicate that the application of glue one segment forward on the abdominal venter had no effect on courtship success in an arctiid (Conner 1987).

DISCUSSION

It is clear that *Haploa clymene* use hydroxydanaidal-laden coremata during courtship and are similar to *Utetheisa ornatrix* L. (Conner et al. 1981), *Pyrrarctia isabella* (J. E. Smith), *Phragmatobia fuliginosa* (L.) (Krasnoff & Roelofs 1990), and *Cisseps fulvicollis* (Hubn.) (Meyer 1984)

in exposing the coremata briefly just prior to contact between the male and female. Coremata exposure appears to be critical to courtship success; in its absence females evade males. The antennae of female *H. clymene* have been shown through electroantennogram bioassay to be sensitive to hydroxydanaidal (Davidson 1995), and thus it is likely that the courtship behavior of *H. clymene* is mediated by the hydroxydanaidal associated with its coremata. The coremata of *H. confusa* also contain hydroxydanaidal and, although courtship studies were not carried out on this species, they likely mate in a similar manner. The order of magnitude difference in the hydroxydanaidal titer between the *Haploa* species is probably related to their dietary differences but further experiments will be necessary to verify this.

Like *Utetheisa* (Conner et al. 1981), *Cretonotus* (Wunderer et al. 1986), *Estigmene*, *Pyrrharctia*, and *Phragmatobia* (Krasnoff & Roelofs 1989) production of hydroxydanaidal in *Haploa* is contingent upon dietary intake of PAs. Yet males reared on diets devoid of PAs have coremata that are visually indistinguishable from those of normal males, in striking contrast to the morphogenetic effects of PAs on coremata development in *Cretonotus* (Boppré & Schneider 1985). The significance of the difference in coremata development between these genera is not yet clear.

Hydroxydanaidal usage is proving to be widespread within the Arctiidae. Hydroxydanaidal (or the related dihydropyrrolizine danaidal) has been identified from the abdominal coremata of *Estigmene acraea* (Drury), *Pyrrharctia isabella*, and *Phragmatobia fuliginosa* (Krasnoff & Roelofs 1989); the genitalic coremata of *Utetheisa ornatrix* (Conner et al. 1981); the abdominal coremata of *Cretonotus gangis* (L.) and *C. transiens* (Wlk.) (Bell & Meinwald 1986); and the abdominal scent brushes of *Paraechaetes pseudoinsulata* Rego Barros (Schneider et al. 1992) within the subfamily Arctiinae, and in the abdominal coremata of *Ciseps fulvicollis* (Krasnoff & Dussourd 1989) and the ventral valve of *Cosmosoma myrodora* Dyar (Ruth Boada, pers. comm.) within the subfamily Ctenuchinae. This broad phyletic distribution for hydroxydanaidal usage in courtship suggests a single evolutionary origin within the Arctiidae. The common ancestor of the Arctiinae, the Pericopinae, and the Ctenuchinae appears to have been a PA-feeder (Jacobsen 1994; Susan Weller, pers. comm.) with, we propose, the ability to produce hydroxydanaidal. We suggest that this single origin set the stage for the repeated evolution of non-homologous scent-disseminating structures throughout the Arctiinae and the Ctenuchinae in a pattern consistent with sexual selection. Although the pericopine *Gnophaela latipennis* (Bdv.) has been shown to contain PAs (L'Empereur et al. 1989) no members of the subfamily Pericopinae have been studied with respect to hydroxydanaidal usage in courtship.

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WHY DO SOME MALE *CALLOPHRYS XAMI* (LYCAENIDAE) SHIFT THEIR TERRITORIES?

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ABSTRACT. In a Mexican population of the butterfly *Callophrys xami* at least 13% of the males defended two or more territories sequentially. There were two observed causes of territory shifts by males: aggressive displacement from their territories by other males ($n = 2$), and spontaneous shift to a different territory ($n = 3$); however, in 26 territory shifts the causes were not determined. Evidence suggests that territories were in short supply during the study and, therefore, more territory shifts may have been the result of aggressive displacement. The spontaneous shifts suggest that some males may move in search of a better territory after occupying one of low quality.

Additional key words: behavioral variation, male competition, territoriality.

In several butterfly species, males defend territories that are employed exclusively for male display, mate location and courtship (Rutowski 1991). Variation in territorial behavior in butterflies has been studied mainly in the context of alternative mate location strategies within a species (Davies 1978, Dennis 1982, Wickman 1985, 1988, Alcock & O'Neill 1986, Dennis & Williams 1987, Alcock 1994), although some authors have also discussed the basis for differences between species in territorial vs. nonterritorial mating systems (Alcock 1985, Dennis & Shreeve 1988, Cordero & Soberón 1990, Wickman 1992).

Although intraspecific variation in the number of territories sequentially defended by male butterflies has been documented (Alcock 1985, Knab 1985, Alcock & O'Neill 1986), it has been specifically discussed in only one study (Robbins 1978). In some species, males spontaneously shift territory as a consequence of their normal migratory movements (Baker 1972). In non-migratory species there are at least two hypotheses to explain territory shifts; these hypotheses and some of their predictions are summarized in Table 1.

In this paper, variation in the number of territories sequentially occupied by individual males of *Callophrys xami* Reakirt (Lycaenidae) is reported, and some of its possible causes and consequences are explored.

MATERIALS AND METHODS

The study was conducted in a 146.8 ha ecological preserve within the main campus of the Universidad Nacional Autónoma de México, in Mexico City. This area is part of the Pedregal de San Angel, and is characterized by volcanic soil, rough topography, markedly seasonal rainfall, and xerophytic shrubby vegetation.

Callophrys xami is a multivoltine butterfly that in the Pedregal de San

TABLE 1. Two hypotheses to explain why males of non-migrant butterfly species might shift territories that they already occupy, and some predictions of these hypotheses.

Hypothesis A: Males shift territories as a result of being aggressively displaced from their previous territories by intruder males.

Prediction A1: Aggressive displacement of territorial males should be observable.

Prediction A2: Successful territory holders (monoterritorial males) should be males with high resource holding power and, therefore, they should tend to be larger, more agile or more experienced than less successful territory holders (polyterritorial males).

Prediction A3: Polyterritorial males, as a result of their displacement from high quality territories, should have a lower copulation success than monoterritorial males.

Prediction A4: The incidence of territory shifts as a result of aggressive displacement should be higher when male density and, therefore, competition for territories is high.

Hypothesis B: Males shift territories because they evaluate their current territories and voluntarily move in search of better ones.

Prediction B1: Voluntary (spontaneous) territory shifts should be observable in territorial males.

Prediction B2: Polyterritorial males should shift, on average, towards territories of higher quality (i.e., those with higher copulation rates).

Prediction B3: Polyterritorial males, as a result of having spent some time in territories of poor quality, should have a lower copulation success than monoterritorial males.

Prediction B4: Male density should be inversely correlated to the probability of finding an unoccupied territory of high quality, and therefore the cost of voluntary territory shift should be lower when density is low, and the probability of changing territory should be higher.

Angel can be found at varying densities throughout the year (Soberón et al. 1988). The population reaches peak density from October to January, although it is never abundant (Soberón et al. 1988). The main larval food plant is the perennial *Echeveria gibbiflora* D. C. (Crassulaceae), which is abundant in the area (Soberón et al. 1988). Males are territorial and defend areas with well defined topographical limits, located beside or on natural or manmade trails; these areas lack concentrations of receptive females and larval or adult food resources (Cordero & Soberón 1990). Males actively defend their territories by means of different types of aggressive flights, for an average of five h per day (between 1000 and 1500), and spend the rest of the time feeding and resting outside territories (Cordero & Soberón 1990). Territories are occupied year after year and function as mate location and courtship stations (Cordero & Soberón 1990, Cordero unpubl. data). Other details of courtship behavior are given in Cordero (1993).

A total of 159 territorial males was captured, individually marked on the wings with indelible felt-tip pens and their right forewing length measured with a caliper through the mesh of the net. Individuals were assigned to one of three wing-wear categories: 1 = similar to a recently emerged adult

(wings mostly green); 3 = very worn male (wings mostly brown with worn margins); and 2 = individuals intermediate between 1 and 3.

Observations were made between 1 November and 20 December in 1989, and between 10 November and 6 December in 1990. The number of territories observed was 25 in 1989 and 19 in 1990; the number of days a territory was visited varied between 25 and 38 in 1989 and between 14 and 24 in 1990. Observations were made in two ways: by walking along transects joining groups of territories at least two times per day, on 31 days in 1989 and 11 in 1990, and observing each territory for a brief time; and by continuous observations through the daily territorial period in a group of occupied territories, during nine days in 1989 and 13 days in 1990.

RESULTS

Most marked males were observed defending only one territory (86/99 males in 1989 and 52/60 in 1990; hereafter, monoteritorial males). Twenty-one males were observed sequentially occupying more than one territory (hereafter, polyterritorial males); these males represented 13.2% of all marked males. Thirteen males occupied two territories, six males occupied three, and two males occupied four. Therefore, a total of 31 territory shifts was detected; however, the exact date of shifts was only determinable for 26 events. The median number of days polyterritorial males occupied each territory was 1 (1.5 in fourth territory, $n = 2$); however, the range varied from <1 day to 14 days in their first territory ($n = 20$), to 1 to 2 days in their fourth territory ($n = 2$) (Table 2). Only one of the 55 marked males observed more than one day in 1983–1985 occupied more than one territory, probably as a result of aggressive displacement (Cordero & Soberón 1990). Territories seem to be in short supply for the males of this butterfly, at least during peaks of male density. In 14 of 17 cases, the site that a male had left was occupied by a different male the same day or the day after.

Direct support for Prediction A1 (Table 1) was provided by two cases in 1989, in which the cause of territory shift clearly was aggressive displacement of the polyterritorial male by an intruder (for description of aggressive interactions see Cordero & Soberón 1990). Two other cases in 1989 probably involved aggressive displacement and resulted in a territory shift. In the first case an aggressive interaction was observed after which a male not previously in the territory began or continued defending it; less than an hour later, the male that had been defending this territory for the three previous days was observed defending a new territory. In the second case, a male was observed for over an hour defending a territory, and then suddenly a different male was in residence; the first male was found defending a different territory 4.5 hours later.

One way of testing Prediction A2 is by comparing the wing length (a measure of size and, possibly, resource holding power) and wing wear (a possible measure of age and experience) of males that are polyterritorial as a result of aggressive displacement with that of monoterritorial males; however, the small number of aggressive displacements observed in this study prevents statistical analysis. In one of three observations of aggressive displacement, the winning male was bigger (1.65 vs. 1.48 cm) and older (2 vs. 1), and in another it was smaller (1.55 vs. 1.62 cm) and younger (1 vs. 3) than the displaced male; data for the third case were not known. Of the two cases of probable aggressive displacement observed in 1989, the winning male was bigger in one (1.72 vs. 1.69 cm) and smaller (1.49 vs. 1.63 cm) in the other. These scant observations neither support nor contradict Prediction A2.

Since virtually all males observed during the course of this and previous studies (since 1983) were territorial or were apparently trying to get a territory, the proportion of territories occupied in a given day was used as a measure of male density (Fig. 1). In 1989, the proportion of territories occupied decreased through the study period ($r_s = -0.887$, $P < 0.001$, $n = 35$), but in 1990 no significant differences were observed in the proportion of territories occupied ($r_s = -0.305$, $P > 0.05$, $n = 17$). Territory shifts were observed throughout the study periods in both years (Fig. 1). Contrary to Prediction A4, aggressive displacement was observed or suspected at both high and low densities in 1989.

Regarding Hypothesis B (Table 1), we observed three cases of spontaneous territory shifts (Prediction B1). In 1989, territorial male *c* moved from territory 3-4S to the contiguous territory 3-4N while inspecting a heterospecific butterfly, and perched in 3-4N without being detected by male *b* (who had been defending 3-4N since the previous day); after two minutes *c* aggressively displaced *b* and defended this "new" territory for the rest of that day as well as the next. No copulations were observed in territory 3-4S, in any of the eight days it was occupied by a male; four copulations were observed in territory 3-4N in the 23 days it was occupied by a male. Also in 1989, territorial male *m* moved spontaneously from territory V to territory IV (about 15 m away) aggressively displaced the previous resident and defended territory IV for one hour, returning afterwards to territory V. Male *m* occupied territory V four more days and later defended territory IV again on two days; this male was observed defending two other territories before defending territory V for the first time. One copulation was observed in the 31 days territory V was occupied; two copulations were observed in the 32 days territory IV was occupied. Finally, in 1990, territorial male 30*a* moved from territory E to territory F' (which was unoccupied), about 25 meters away, and defended it for one day. This male was observed again defending territory

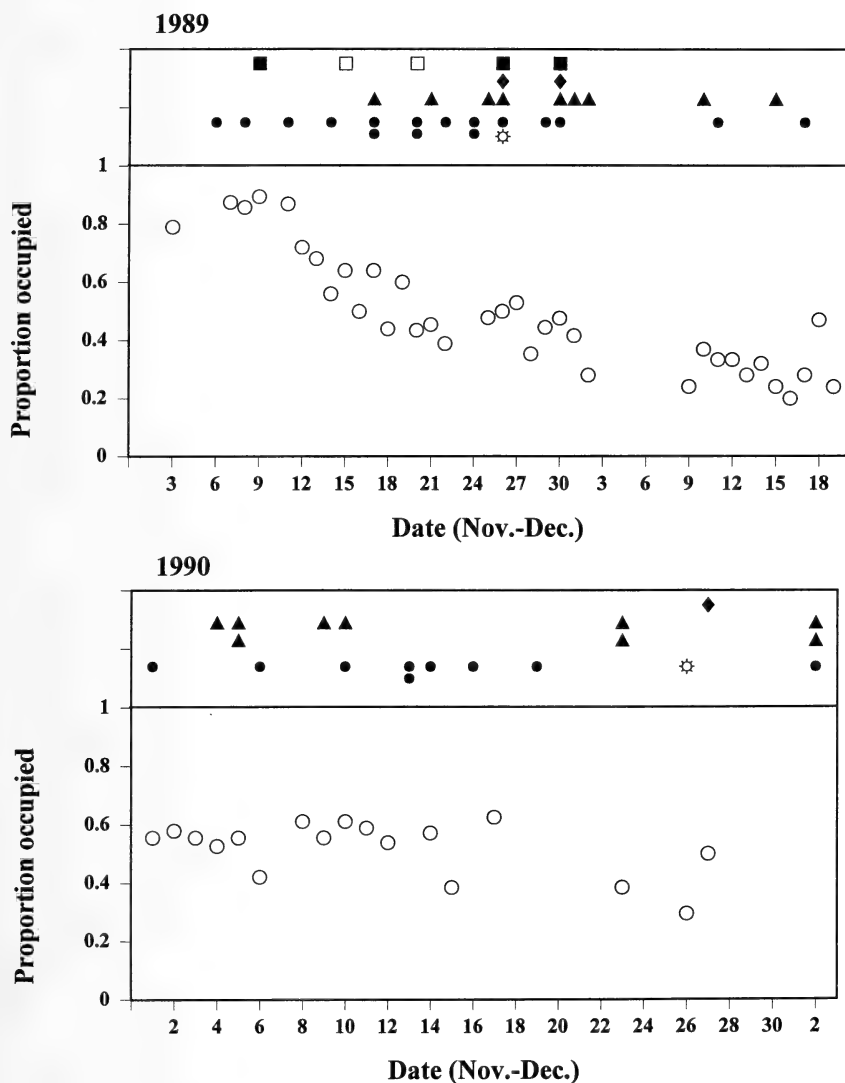


FIG. 1. Proportion of territories occupied by males, territory shifts and matings observed during the study periods of 1989 and 1990. In 1989, only those days in which 17 or more territories were surveyed are included; in 1990, only those in which 13 or more territories were surveyed are included. Key: *solid squares*: observed aggressive displacements; *empty squares*: suspected aggressive displacements; *diamonds*: spontaneous territory shifts; *triangles*: territory shifts due to unknown causes; *solid circles*: matings by monoterritorial males; *sunbursts*: matings by polyterritorial males; *empty circles*: proportion of territories occupied

TABLE 2. Summary of male characteristics. WL: wing length (cm). WW: wing wear category. L: longevity (days). T₁, T₂, T₃ and T₄ are, respectively, the number of days polyterritorial males defended their first, second, third and fourth territories. Cop: number of copulations.

	WL	WW	L	T ₁	T ₂	T ₃	T ₄	Cop
All males:								
mean \pm SD	1.64 \pm 0.1	1.56 \pm 0.73	4.8 \pm 5.4	2.4 \pm 3	2 \pm 2	2.7 \pm 2.5	1.5 \pm 0.7	0.15 \pm 0.5
median	1.65	1	2	1	1	1	1.5	0
range	1.36-1.89	1-3	1-28	<1-14	<1-9	1-7	1-2	0-4
N	145	147	156	20	20	8	2	159
Males shifting via aggressive displacement:								
<i>g'</i>	1.62	3	7	4	<1	—	—	1
<i>y</i>	1.76	1	1	<1	1	—	—	0
Males shifting spontaneously:								
<i>c</i>	1.65	2	2	<1	2	—	—	0
<i>m</i>	1.55	1	17	1	1	5	2	0
30a	1.59	2	7	4	1	1	—	0

E on two days, four days after defending territory F'; afterwards he occupied territory A for one day. No copulations were observed in any of the six and four days territories E and F', respectively, were occupied. The fact that two spontaneous shifts were toward territories which apparently had higher copulation rates is in agreement with Prediction B2. The behavior of the last two males suggest sampling of territories, an idea implicit in Hypothesis B.

In agreement with Prediction B4, the two spontaneous territory shifts witnessed in 1989 occurred when male density was low (Fig. 1). In both years, spontaneous shifts were observed in the second half of the study period and after most of the copulations were observed (Fig. 1), suggesting that a decreasing encounter rate with females may be used by males as a cue for voluntarily leaving the territory.

Only two polyterritorial males were observed copulating, both in their second territory; these males were observed defending two territories and the causes of their territory shifts are unknown (one of these males was aggressively displaced from his second territory a few minutes after mating finished, and returned to his first territory).

DISCUSSION

In *Callophrys xami* some males shift territory because they are aggressively displaced from their territories by other males, or because they move spontaneously to a different territory. Given that the cause of 84% of the territory shifts detected was unknown, the relative importance of each of these causes cannot be determined.

The direct observations of aggressive displacement indicate that competition for territories is an important cause of shifts between territories. Rapid re-occupation of abandoned territories also suggests intense competition for territories. Competition happens in spite of the availability of unoccupied territories (Fig. 1), suggesting that competition varies in space at a local scale, probably in response to limited male movement and differences in territory quality, and, temporarily, due to local changes in male density and territory quality.

The existence of spontaneous territory shifts indicates that factors other than aggressiveness are responsible for some of the shifts. One possibility (Hypothesis B) is that males shift towards territories of higher quality (i.e., where mating rates are higher). We have insufficient data to test this possibility; however, the two observed copulations of polyterritorial males occurred in their second territories. Furthermore, two spontaneous shifts were towards territories where copulation rates seemed to be higher.

If the quality of prospective territories is difficult to determine for a male butterfly, males may simply tend to move to a different territory in

the hope of finding a better one. The time spent in a territory that is eventually abandoned may be necessary to determine its low quality or it may reflect a territory quality changing (decreasing) with time. Under these conditions we would expect to observe some cases of males shifting territory and returning to the previous one after some time, as was observed in two cases. Under this scenario, a smaller, and therefore more difficult to detect, difference between the average quality of pairs of territories sequentially occupied by males changing spontaneously might be expected. Intensive studies are needed to analyze the possible effects of territory characteristics on territory shifts.

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EGG CANNIBALISM BY NEWLY HATCHED LARVAE OF THE SMALL WHITE BUTTERFLY, *PIERIS RAPAE CRUCIVORA* (PIERIDAE), ON AN ARTIFICIAL DIET

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ABSTRACT. Newly hatched larvae of the small white butterfly, *Pieris rapae crucivora*, wandered over an artificial diet without feeding for ca. 2 hrs after eating their own egg shells. When they encountered unhatched conspecific eggs, egg cannibalism occurred. Throughout the first instar, larvae fed on eggs and intermittently on the artificial diet. The duration of the first instar was significantly shorter for cannibals than for non-cannibals. As later first instars, the cannibals wandered randomly and only nibbled unhatched eggs. Egg cannibalism may help larvae exclude potential rivals from competing for nutrients when the host plant in the field is a limited resource. Because females lay eggs singly and seldom return to oviposit on the same host plant, siblicide in the field is presumably rare or absent.

Additional key words: artificial diet, devouring, larval duration, nibbling, starved larvae.

Females of the small white butterfly, *Pieris rapae crucivora* L., deposit their eggs on the exposed leaves of cruciferous plants. Parasitic wasps, bugs, mites and ants have been recognized as major agents of egg mortality for pierid butterflies on cabbage (e.g., Harcourt 1966, Parker 1970, Feltwell 1982) and on field cress, *Rorippa indica* Hiern (Yamaguchi & Watanabe 1993). Courtney (1986) pointed out that cannibalism is also a major cause of mortality in most Pierinae.

In general, the newly hatched larvae of pierid butterflies eat their own egg shell before eating their host plants. However, the earliest hatched larvae often devour unhatched eggs on the same leaf (Rausher 1979, Watanabe & Yamaguchi 1993). Brower (1961) stated that eating egg shells may simply represent opportunistic egg cannibalism. Since egg cannibalism has been observed in high egg density, the behavior of larvae cannibalizing eggs has been regarded as abnormal (e.g., Feltwell 1986, Warren 1992). However, cannibalism can strongly affect population density when resources are limited (e.g., Fox 1975), and show a density-dependent effect on population dynamics (Polis 1981, Elgar & Crespi 1992). The cannibalistic behavior of newly hatched larvae that occurs under crowded conditions in the absence of sufficient food has been reported in many species (e.g., Dempster 1983). When reared under crowded conditions, larvae of the orange tip, *Anthocaris cardamines* L., showed cannibalistic behavior (Feltwell, 1986).

Egg cannibalism by larvae has been observed under conditions of nutritional deprivation in the laboratory (Hayes 1982). Stenseth (1985) concluded that cannibalism may evolve as the result of individual selec-

tion even in cases where food resources are not in extreme shortage. However, Shapiro (1981) found that egg cannibalism frequently occurred for *P. protodice* Boisd., in which a mechanism of avoiding oviposition on the same leaf surface may have evolutionary implications. Watanabe & Yamaguchi (1993) found that intra- and inter-specific cannibalism among pierid butterflies involved eggs and newly hatched larvae on the same leaf in the field.

The present study was designed to provide insight into the mechanism of egg cannibalism by *P. rapae* under constant substrate conditions.

MATERIALS AND METHODS

Pieris rapae females were collected mainly in Nagano Prefecture, in the cool-temperate zone of Japan, during the summer of 1993. Mated females were obtained from the field and were allowed to deposit eggs on cabbage leaves. Eggs were laid during 2 h around noon on each sampling day.

About 24 h after oviposition, each egg was placed on a medium containing artificial diet (Sato 1974) in a petri dish kept at room temperature (ca. 25–30°C). Wet filter paper approximately 8 cm in diameter was placed on the floor of each dish to reduce desiccation. Some eggs were placed on the wet filter paper for subsequent comparison of larval behavior with that on the artificial diet. All of the eggs were in late developmental stages, as identified by their egg color (yellowish orange). A detailed description of the developmental stages of eggs is given by Watanabe et al. (1993).

Eggs offered to newly hatched larvae were derived from females placed on leaves on subsequent days. None of these eggs hatched earlier than the hatched larvae. Every egg was placed vertically on the food medium or filter paper like a naturally deposited egg. The arrangement of these eggs on the artificial diet in a petri dish is shown in Fig. 1. The number of eggs offered as food was 36 for each egg cannibalizing experiment. Twenty hatched larvae were tested. Since Watanabe & Yamaguchi (1993) found that the average distance between eggs deposited on a leaf of field cress, *R. indica*, was ca. 8 mm in the field, in this experiment all the eggs were placed 8 mm apart from each other.

The position of each cannibalized egg was determined by counting the number of 'steps' from the previously cannibalized egg. A step represents the space between eggs i.e., the distance measured in number of 8 mm units, because we did not know the actual distance of the route of the larva during 10 min observation intervals. For the first egg cannibalized, the location was the number of steps from the original point where the larva hatched.

A stereoscopic microscope was used to observe each larva every 10

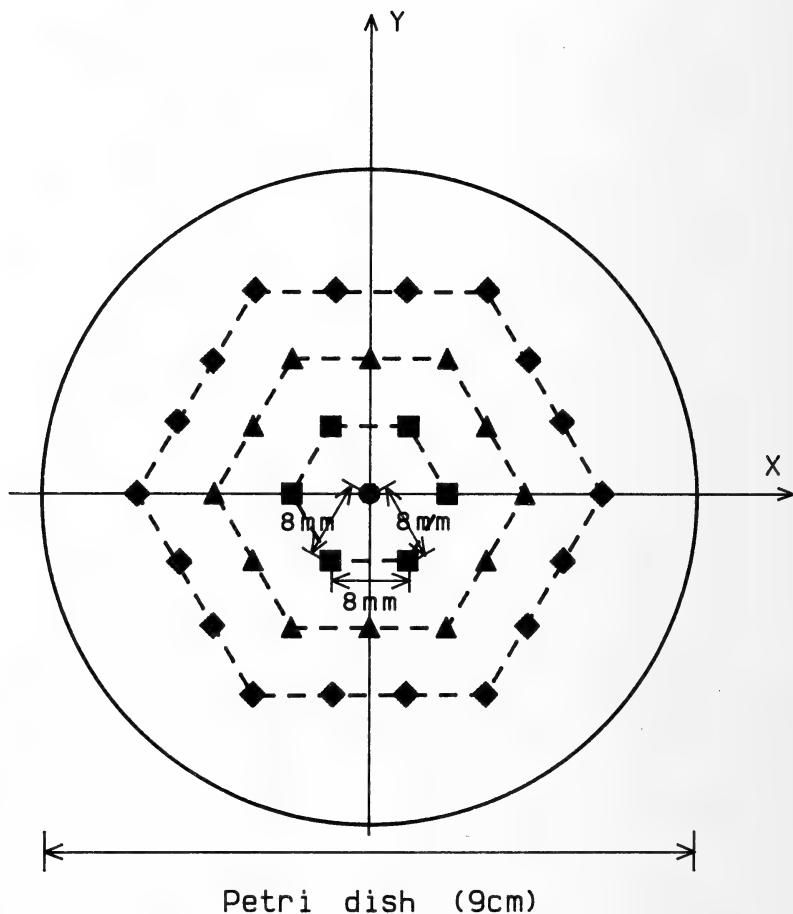


FIG. 1. Arrangement of eggs placed on artificial diet in 9 cm diam. petri dishes. Filled circle indicates an egg that will hatch first and become the cannibal. Squares, triangles and diamonds represent eggs 1, 2 and 3 steps away from the cannibal, respectively.

min, from hatching to the first molting. Records were made of larvae feeding on their own egg shells, on the artificial diet, and on other eggs. Time spent moving between eggs and resting was also recorded. Larval position was recorded every 10 min, in relation to the position of the egg from which the larva hatched.

RESULTS

Immediately after hatching, all 20 larvae began to eat their own egg shells. This normally took about 90 min (Table 1). The larvae then moved out onto the artificial diet.

TABLE 1. Time elapsed for each feeding behavior from the time of hatching, for cannibal and non-cannibal larvae of *Pieris rapae*. Values are minutes \pm SE, and are based on 21 cannibal and 5 non-cannibal larvae. Asterisks denote significance at $p < 0.05$ for cannibals vs non-cannibals.

Feeding behavior	Cannibals	Non-cannibals
end of feeding on own egg shell	97 \pm 11.1	88 \pm 18.5
start of feeding on first egg	179 \pm 20.3	—
start of feeding on artificial diet*	387 \pm 56.7	174 \pm 17.8
duration of first instar*	3701 \pm 179.8	4863 \pm 133.8

Larvae that were not presented with eggs (i.e., solitary larvae) began to feed on the artificial diet about three hours after hatching. The yellow-brown mid-gut became greenish due to the color of the artificial diet. The larvae then wandered about on the diet, feeding intermittently, during the first instar stage. The duration of the first instar was about 82 h (=3.4 days).

Newly hatched larvae that were presented with eggs began to eat the first egg three hours after hatching. This was not significantly different from the starting time of feeding on artificial diet by solitary larvae (=non-cannibals). The mid-gut remained yellowish brown for some time because they had not yet fed on the artificial diet. There was a delay before the start of feeding on the artificial diet. The mid-gut of cannibal larvae did not become greenish until 6.5 h after hatching. This was significantly longer than the onset of greenish color in solitary larvae ($P < 0.05$ by F-test). Cannibal larvae wandered about with less feeding than solitary larvae. The duration of the first instar of the cannibals was significantly shorter ($P < 0.05$ by F-test).

The newly hatched larvae fed on neighboring eggs (= 1 step) and then fed on eggs 2 steps away. As shown in Fig. 2, one of 20 larvae fed on 2 eggs during the first instar stage, while another fed on 19 eggs (larvae fed on 8.3 ± 4.7 eggs (SE) on average). Because the number of eggs offered as food was stable and they were evenly spaced, it can be seen from the data that, within the limitations of our method, cannibalism may not be a mortality factor in relation to density of unhatched eggs.

Egg cannibalism first occurred 179 ± 20 min after hatching ($n = 14$). All of the larvae ate eggs within one step. The second egg was eaten by the larvae 421 ± 80 min after hatching ($n = 15$), and thereafter the third 532 ± 89 min ($n = 13$), the fourth 773 ± 112 min ($n = 13$), and the fifth 1108 ± 204 min ($n = 13$). The time elapsed between each cannibalism event was thus 100–300 min. The tenth egg cannibalism was observed 1618 ± 95 min after hatching ($n = 4$). Larvae that were more than one day old displayed short intervals between cannibalism events. They moved out one step, and attacked adjacent eggs. The most active larva

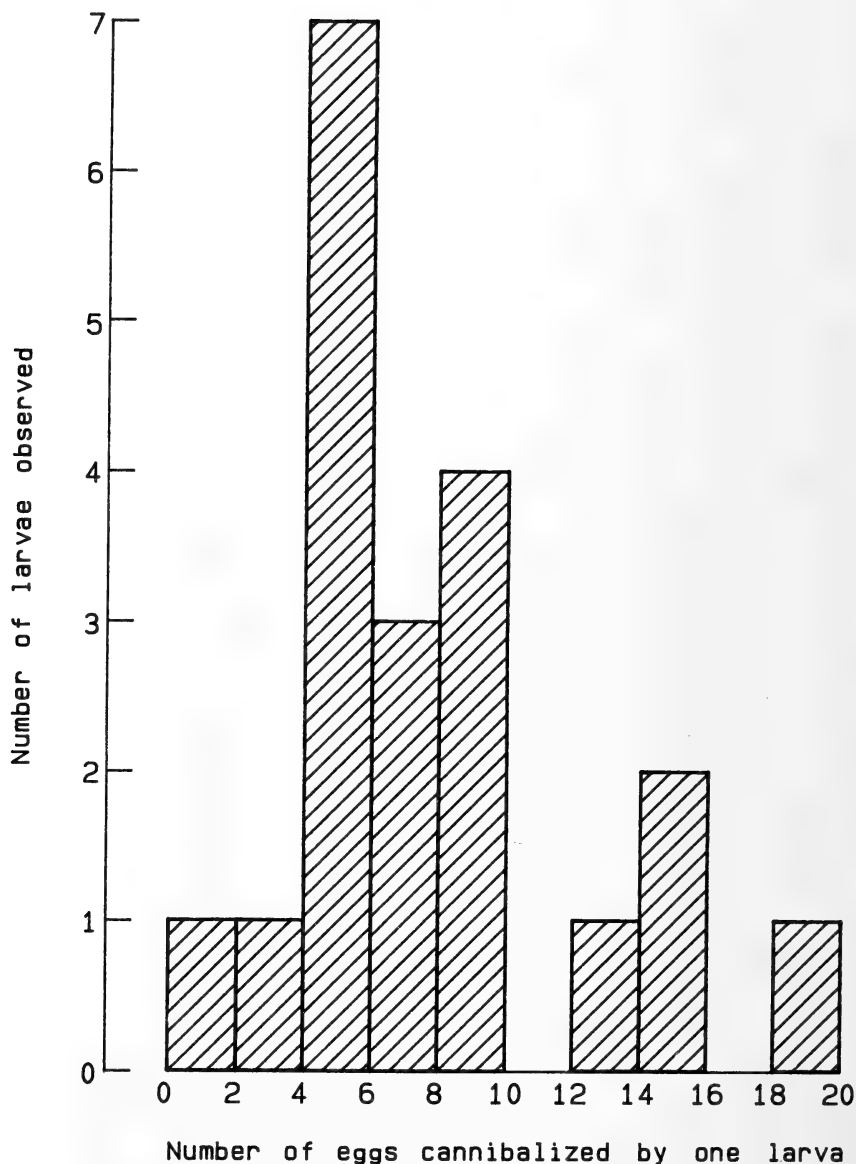


FIG. 2. Frequency distribution of the number of eggs cannibalized.

ate 19 eggs in 3520 min after hatching. The results show that larvae can and do eat conspecific eggs throughout the first instar stage.

After eating their own egg shells, movement by solitary larvae increased to 13 mm/min (Fig. 3). Slower movement reflected the time

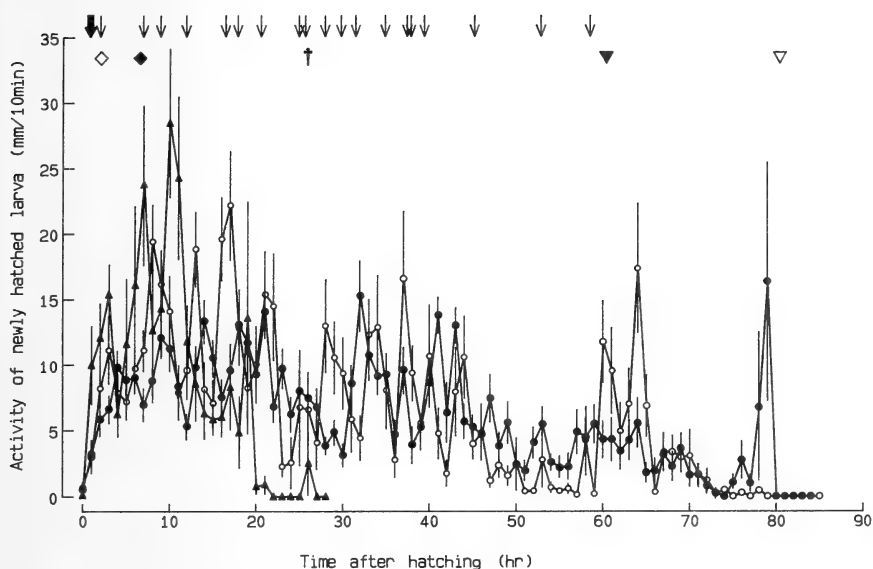


FIG. 3. Changes in movement by first instar larvae on artificial diet (\pm SD). Dots, open circles and small triangles represent cannibals, non-cannibals and starved larvae, respectively. Thick arrow shows average time required for larvae to eat their own egg shells. Each thin arrow indicates the average of each starting time for cannibals. Closed and open diamonds show the average starting times for feeding on artificial diet by cannibals and non-cannibals, respectively. Closed and open triangles indicate the average molting time to the second instar for cannibals and non-cannibals, respectively. Cross shows average time of death of starved larvae.

taken for feeding on the diet and intermittent resting. Movement by larvae over 45 h old decreased to 5 mm/min. The older larvae often rested, and then molted into the second instar. The speed of movements of cannibal larvae was generally similar to that of solitary larvae, but there were several high peaks of movement by cannibal larvae (Fig. 3). On average, the cannibal larvae were more active than solitary larvae.

Larvae hatched on the wet filter paper began to wander in the petri dish after eating their own egg shells. Their movement was the fastest. They were most active until 12 h after hatching. Their speed decreased gradually thereafter, and they became inactive after about 20 h. The average longevity of the starved larvae was about 26 h (≈ 1.1 days).

The distance moved by larvae increased with time after hatching. As shown in Fig. 4, the change in the cumulative distance differed for cannibal and solitary larvae (Kolomogorov-Smirnov test, $0.05 > P > 0.01$). The cannibals moved further than the non-cannibals during the first 20 h after hatching. However, both moved about 3000 mm during the first instar. A rapid increase in distance moved by the starved larvae was ob-

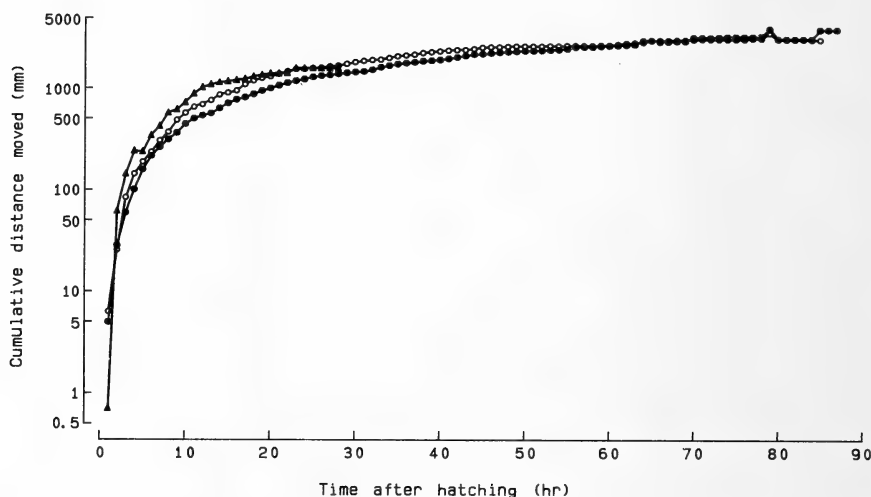


FIG. 4. Changes in the accumulated distance moved for first instar larvae on artificial diet. Dots, open circles and small triangles represent cannibals, non-cannibals and starved larvae, respectively.

served on the wet filter paper. The cumulative distance moved differed significantly (Kolomogorov-Smirnov test) from the distances for cannibal larvae ($P < 0.01$) and the larvae on artificial diet ($P < 0.01$). The starved larvae moved 1000 mm during their life span.

The duration of feeding on a single egg also varied. It took a cannibal larva more than 20 min to consume an entire egg. Some larvae devoured the entire egg with intermittent resting, which increased the time required for complete consumption. As shown in Fig. 5, there were a few larvae that finished eating the first egg within 20 min, but most spent much more than 20 min to consume the egg. Other larvae only nibbled parts of a victim egg shell before beginning to wander. Partial nibbling on an egg usually lasted less than 15 min. Fig. 5 also shows that most cannibal larvae did not spend much time to contact more than 10 eggs. There was a significant tendency for time spent cannibalizing to decrease with the number of unhatched eggs encountered. Therefore, most cannibal larvae tended to devour entire eggs at the onset of feeding, and then nibble eggs later. All eggs that were nibbled did not develop further and did not produce larvae.

Between the first to the fifth eggs cannibalized, larvae usually devoured or nibbled an egg that was nearest (Fig. 6). The large average step number means that larvae moved long distances while feeding on eggs, and apparently sometimes ignored neighboring eggs while moving out randomly on the artificial diet.

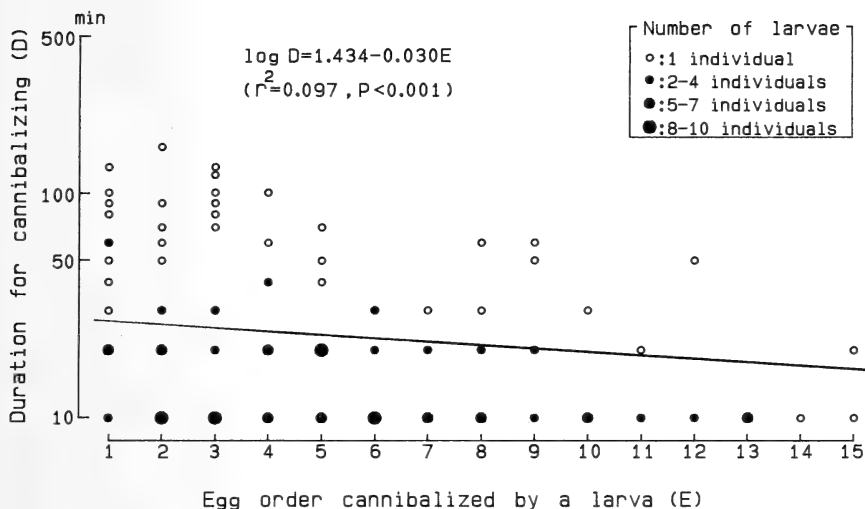


FIG. 5. The relationship between the egg order cannibalized and the duration of cannibalizing.

DISCUSSION

The present experiments show that larvae of *P. rapae crucivora* have a high propensity for egg cannibalism under laboratory conditions throughout the first instar. The newly hatched larvae wandered over the artificial diet without feeding, or on wet filter paper, for two hours after eating their own egg shells (newly hatched larvae also tend to wander actively on host plant leaves in the field i.e., they seem to search for eggs on the leaves similar to their behavior on the artificial medium in this experiment; Watanabe, unpubl. data). While wandering on artificial medium, larvae attack eggs that are encountered. If the larvae cannot find eggs, they begin to feed on the artificial diet. Watanabe and Yamaguchi (1993) found that larvae on leaves with conspecific eggs behaved as cannibals before starting to eat leaves in the field.

Larvae did not feed on the artificial food medium for two hours after hatching, but wandered. They may waste energy during this period. However, starved larvae were able to wander actively on wet filter paper for 12 h. Therefore, newly hatched larvae may not be adversely affected by failing to feed during their first two hours, as this time may be for locating eggs in the field.

Two kinds of egg cannibalism were seen: consumption of the entire egg, and nibbling of part of the egg shell. Both kinds of cannibalism were fatal to unhatched larvae. The former presumably provides the cannibals with nutrients, whereas nibbling may exclude unhatched con-

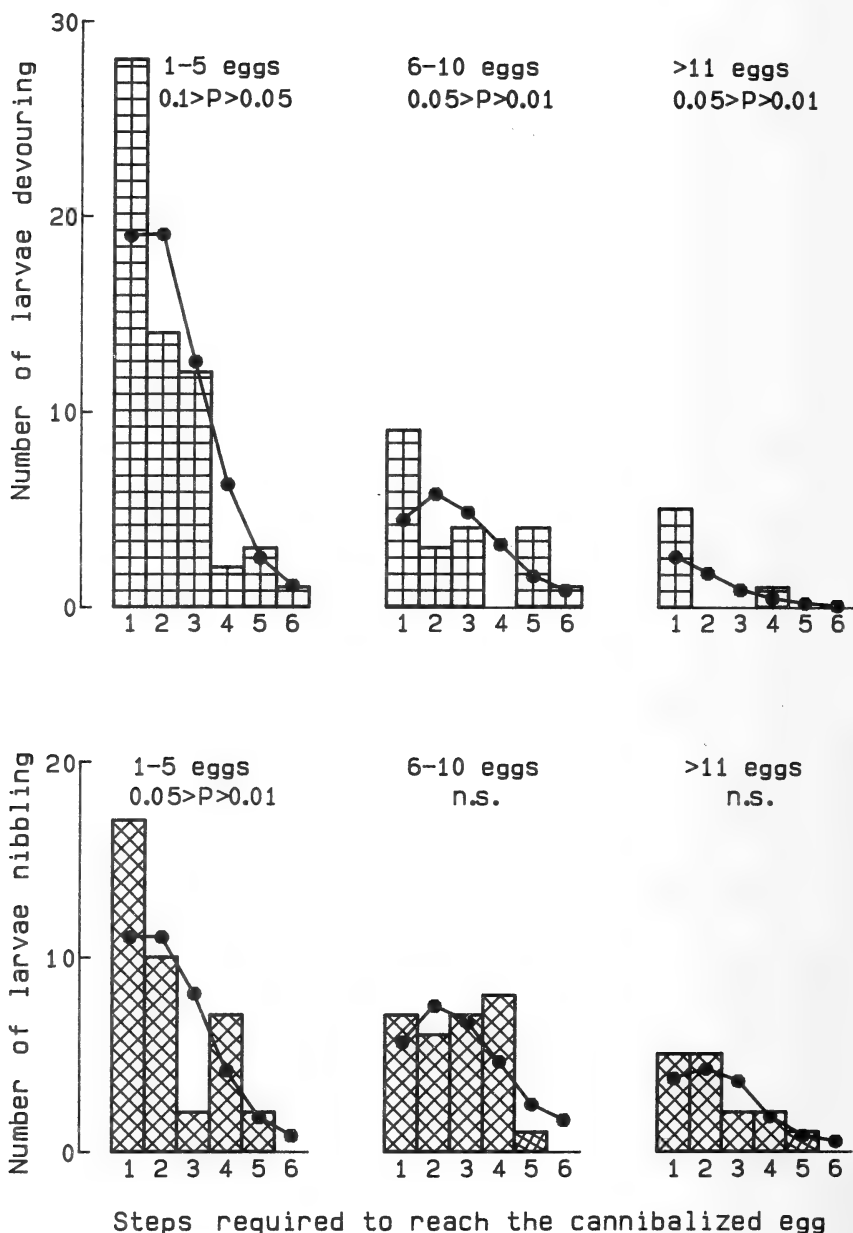


FIG. 6. Frequency distributions of the step-number of eggs cannibalized. 1-5, 6-10, >11 eggs mean the order of eggs cannibalized. Dots show the Poisson distribution. See text for further elaboration.

specifics that would otherwise be competing for food. Therefore, possible advantages for the cannibal include both nutrient gain and the elimination of competitors (Baur & Baur 1986).

Eggs of *P. rapae crucivora* contain amino acids and organic compounds that are not directly derived from leaves (Porter 1992). Such materials might facilitate larval development during the first instar. Cannibalism increases the growth rate of larvae that eat eggs (e.g., Dickinson 1992, Agarwala & Dixon 1992). Osawa (1992) stated that first instar larvae of the lady beetle, *Harmonia axyridis* Pallas, developed faster after eating conspecific eggs. In *P. rapae crucivora*, however, there were no significant differences between cannibalizing and non-cannibalizing larvae over the whole larval period with regard to adult size and weight, or female fecundity (Watanabe, unpubl. data). We observed no egg cannibalism by second, third, fourth and fifth instar larvae, despite Yamamoto's (1981) finding that the eggs of *P. rapae crucivora* and *P. napi* L. were eaten by older larvae.

Courtney & Courtney (1982) stated that cannibalism is concentrated upon particular host individuals, because of contagious egg distributions. Brower (1961) stated that egg cannibalism is density-dependent in the case of the Queen butterfly, *Danaus gilippus*. Polis (1981) noted that cannibalism can also be a tactic to gain exclusive use of resources that serve as both food and habitat. For larvae, there are advantages in being single: more food, and less chance that other members of the same family group will become parasitised or eaten at the same time (Feltwell 1986). The proportion of eggs surviving was a function of larval density in an Australian population of *P. rapae* (Jones & Ives 1979). Watanabe & Yamaguchi (1993) observed that, as a rule, a single larva settled on a single leaf of the field cress, *R. indica*, suggesting that newly hatched larvae may have consumed unhatched eggs on the same leaf.

Egg cannibalism in *P. rapae crucivora* may be advantageous for larval survival on limited resources as well as for the intake of nutrients. While devoured eggs were usually those nearest to the larva, nibbled eggs (>6th eggs) were distributed randomly. The first instar larvae seemed to wander not to take eggs for nutrients, but to kill potential conspecific competitors. Cannibalism helped cannibals when food density was low (e.g., Osawa 1992), because the relatively small host *R. indica* is heavily damaged by a single larva over its complete life cycle (Yano 1993).

Most eggs of *P. rapae* are deposited on the under surface of leaves (Yamamoto 1985 observed that 97% of females deposited eggs on the undersides of leaves of the field cress, *R. indica*). This may induce oviposition by more than one female on the same leaf. In fact, Watanabe and Yamaguchi (1993) counted 781 field cress leaves that had eggs, and found that 25% of them received more than one egg. This presumably

means eggs from more than one female. However, no evidence was obtained for segregation of females on different host plants.

Ohtani & Yamamoto (1985) found that females of *P. rapae* have no site fidelity, emigrating from their emergence site. Since the females lay eggs singly and seldom return to deposit on the same host plant (Watanabe & Yamaguchi, unpubl. data), eggs on the same leaf may be deposited by two or more females. Porter (1992) stated that single-egg-laying females distribute eggs over a large number of host plants, and that this spreads the risks of predation and cannibalism, and reduces competition with other larvae. Rothschild & Schoonhoven (1977) concluded that *P. rapae* discriminated between a cabbage leaf from which conspecific eggs had been removed and a clean control leaf. Few accounts of butterfly cannibalism have considered kin relatedness (e.g., Courtney 1986), though Jones (1982) reviewed cannibalism in relation to kin selection.

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NOTES ON HESPERIIDAE IN NORTHERN GUATEMALA, WITH DESCRIPTIONS OF NEW TAXA

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ABSTRACT. Several significant records of HesperIIDae were obtained in the vicinity of Parque Nacional Tikal, northern Guatemala. A new genus, *Vinpeius*, is proposed for *Pompeius tinga* Evans (= *Vinius freemani* L. Miller). Another new genus, *Inglorius*, is proposed for a newly described species, *Inglorius mediocris*. *Niconiades incompus*, similar to *Niconiades xanthaphes* Hübner, is described as a new species. Range extensions are reported for *Methionopsis dolor* Evans, *Mnasitheus nitra* Evans, *Parphorus storax* (Mabille), *Styriodes zeteki* (Bell), *Phlebodes campo* Evans, *Euphyes antra* Evans, *Amblyscirtes tolteca* Scudder, *Aides brilla* (Freeman), *Ridens allyni* Freeman, *Cyclosemia leppa* Evans, and *Staphylus lenis* Steinhauser. Genitalia are illustrated for many of the foregoing, including variation in the harpes of *Nisoniades rubescens* (Möschler).

Additional key words: Central America, distribution, genitalia, Neotropics.

The butterflies of Guatemala are poorly known. Except for reports on a few old collections (Boisduval 1870, Godman & Salvin 1879–1901, Gibbs 1912), nearly nothing has been published on this fauna. A survey and monitoring study in the Parque Nacional Tikal region, Petén Department, northern Guatemala, has produced numerous interesting records (Austin et al. 1996), many of which represented species not previously recorded for the country. Most of these were known from surrounding countries, but others extended distributions considerably southward or northward, sometimes spectacularly. Miller (1985) observed that several butterfly species exhibited apparently broad disjunctions between southern Central and South American populations and those in Mexico similar to those noted below. I will herein discuss significant extensions of known ranges among skippers (Hesperiidae), propose two new genera of Hesperinae, and describe two new species.

HESPERIIDAE

Vinpeius Austin, new genus

Type species: *Pompeius tinga* Evans, 1955

Description. Palpi slender, third segment protruding about 1/2 length of second, pale yellow-orange with scattered black scales; antennae long, reaching beyond end of discal cell, nearly 60% of costal length, yellow beneath club and on most of ventral surface of shaft except narrowly black at segments, club 1/3 shaft length, bent to apiculus after thickest part, apiculus length 1.5× width of club, nudum brown, of 14 segments (6 on club, 8 on apiculus); forewing discal cell somewhat produced anteriorly, just over 75% length of anal margin, vein CuA₂ arises somewhat nearer origin of vein CuA₁ than to base of wing, hindwing discal cell about 1/2 width of wing; mid tibiae spined on inner surface and with one pair of terminal spurs, hind tibiae with two pairs of spurs; forewing somewhat produced, costa very slightly concave just before middle, termen evenly convex, stigma along

cubitus from origin of vein CuA_1 nearly to origin of CuA_2 where bent posteriad across vein CuA_2 to 1/2 distance to vein 2A where angled proximad again nearly reaching 2A, composed of numerous fine gray hair-like scales interspersed with shorter spine-like black scales, these continuous along anterior edge where adjoining cubitus, entire stigma narrowly surrounded by unmodified, but semierect brown scales, these extending from stigma to base of cell CuA_1 - CuA_2 ; hindwing evenly convex except slightly indented in cell CuA_2 -2A. Male genitalia with tegumen short, but with central spur which extends caudad over uncus; uncus short, blunt, broad, not divided; gnathos short, not reaching end of uncus, divided, arms convergent; vinculum nearly straight; saccus moderately long; valva broad; costa/ampulla margin gradually ascending caudad; harpe very broad; caudal margin excavate ventrad, dorsal margin triangular with narrow tooth-like projection dorsad from inner surface barely exceeding dorsal margin; aedeagus tubular with long (about 2/5 total aedeagus length), narrow, and spinate caudal projection from lower right side; no cornutus.

Etymology. The name is a combination of parts of the names of the two genera in which the included species was previously placed, *Vinius* Godman, 1900 and *Pompeius* Evans, 1955.

Diagnosis. A full diagnosis is given below under the one included species of *Vinpeius*.

***Vinpeius tinga* (Evans, 1955), new combination**
(Fig. 11)

Pompeius tinga Evans, 1955

Vinius freemani L. Miller, 1970, **new synonymy**

Pompeius freemani de la Maza et al. 1991, **new synonymy**

A male hesperiine taken south of Parque Nacional Tikal and east of Coaba on 1 Oct. 1994 initially defied generic determination using the keys of Evans (1955). The genitalia of this specimen, however, resembled one species illustrated by Evans (1955), *Pompeius tinga*, and the description given in the accompanying text confirmed this identification (note that the Evans figures of the tegumen, uncus, gnathos, and aedeagus are different from those shown herein and by Miller [1970]; the uncus and gnathos of the Evans specimen were evidently lost in dissection and only the tegumen and aedeagus were illustrated). A further search of the literature from surrounding countries indicated that this taxon was redescribed by Miller (1970) as *Vinius freemani*. The Tikal male matches this taxon perfectly in wing pattern and genitalia.

The characters of *Vinpeius tinga* are neither those of *Pompeius* nor *Vinius*. Evans (1955) included *Pompeius* in his "Hesperia Sub-group" of the "Hesperia Group" of hesperiines and characterized the genus as having the antenna nearly 1/2 the length of the costa with the club 1/4 the length of the antennal shaft, an apiculus equalling the width of the antennal club, a nudum of 13 segments with 6 or 7 of these on the apiculus, and a well-marked black stigma on the dorsal forewing. Examination of the type species, *Pompeius pompeius* (Latreille, [1824]), indicated that this diagnosis needed some embellishment. The nudum of *P. pompeius* varies from 13 to 14 segments arranged as 7 on the club and 6

($n = 8$) or 7 ($n = 2$) on the apiculus. It should be noted here that the antennal segments vary in number and are difficult to count (e.g., Burns 1964, MacNeill 1964), especially in distinguishing between those on the club and those on the apiculus (Steinhauser 1981). The blunt third segment of the palpus barely protrudes from the scales of the second segment. The mid tibiae are conspicuously spined on both the outer (stout, short) and inner surfaces (stout, long). The origin of vein CuA_2 is barely distad of the midpoint between the wing base and vein CuA_1 . The stigma is conspicuous and complex extending from the base of vein CuA_1 to nearly the base of CuA_2 and then posteriad to vein 2A. The anterior edge along vein CuA_1 consists of relatively dense, small, spike-like black scales. Posterior to this is an area of dense, hair-like, gray scales which curves posteriad across CuA_2 and extends nearly to 2A. This gray area has scattered black scales and is margined posterio-distad by a narrow line of spike-like black scales. A more or less round patch of these black scales also occurs at the posterior end of the gray area; this is the "lower brush patch" of MacNeill (1964). Distad of this is a large area of somewhat modified shiny scales extending posteriad from near the base of CuA_1 , bulging outward at CuA_2 and angling proximad to 2A. Similar scaling occurs in the base of CuA_1 - CuA_2 and in the postbasal area of CuA_2 -2A.

The male genitalia (see figures in Godman & Salvin 1879-1901, Hayward 1951, Evans 1955) consist of a long and relatively narrow tegumen (V-shaped on the posterior edge in dorsal view), divided uncus with long and narrow arms in lateral view and narrowly pointed in dorsal view, and divided gnathos with long and narrow arms in lateral view with the tips laterad of the uncus arms in dorsal view. The vinculum is slightly curved and the saccus is short. The valva has a sharply sloping cephalad end, a prominent dorsal spike from the harpe, and the sacculus gradually narrows caudad extending nearly to the caudal end of the harpe. The aedeagus is tubular and the caudal end has short lower and lateral lips, the latter with thorn-like teeth. The two cornuti are short, tubular, and prominently dentate.

Of the six additional species included by Evans (1955) in *Pompeius*, I examined three. *Pompeius amblyspila* (Mabille 1897) is very similar to *P. pompeius* in numerous characters including antennae (nudum 7/6), stigma, and genitalia (figured by Bell 1932, Hayward 1951, Evans 1955). *Pompeius verna* (Edwards 1863), including its two subspecies, *P. v. verna* and *Pompeius verna sequoyah* (Freeman 1942), is somewhat different and may belong to another genus. The nudum is 6/7, the stigma is less complex and extensive and without a "lower brush patch," and the genitalia (figured by Scudder 1889, Lindsey et al. 1931, Evans 1955) are very different, including a shorter and stouter tegumen with a shallow

V-shape cephalad in dorsal view, a shorter and blunter uncus in both lateral and dorsal view with the arms not proximate in dorsal view, the gnathos much narrower than the uncus, and the cornutus an inconspicuous long and filament-like structure. "*Pompeius*" *tinga* is discussed above and below.

The taxa included in the "Vinius Group" by Evans (1955) either lack androconial structures on the forewing or have brands except for one genus (*Wahydra* Steinhauser, [1991]) with a stigma. *Vinius* was characterized (Evans 1955) by antennae longer than 1/2 the costa length with the club 1/4 the length of the shaft, a nudum of 13 segments of which 10 are on the apiculus, spined mid tibiae, males with short brands above and below the middle of vein CuA_2 , and an erectile hair tuft along vein 3A on the dorsal hindwing with a groove in the same position of the ventral hindwing. Additional characteristics include an apiculus which is about $2\times$ club width, the sharply pointed third segment of the palpus extends beyond the scales of the second segment by about 1/4 the length of the second segment, the mid tibial spines are fine and on the inner surface, and the origin of forewing vein CuA_2 is much closer to CuA_1 than to the wing base. The male genitalia (e.g., figures by Godman & Salvin 1879–1901, Williams & Bell 1934, Evans 1955, Mielke 1968, Biezanko & Mielke 1973) have a short tegumen, a blunt uncus that is short, broad, and not divided, a short and divided gnathos with parallel arms, a strongly curved vinculum, and a short saccus. The valvae of *Vinius* are variable with the harpe caudally sloping or having a toothed dorsal margin. The aedeagus is tubular and with no prominent caudal extensions or cornutus.

The antennae of *Vinpeius tinga* are proportionately longer than on *P. pompeius* and about the same as on *Vinius* and the antennal club is longer than on either genus. The nudum of *Vinpeius* has 14 segments (one more than either *Pompeius* or *Vinius*) with eight of these on the apiculus (more than the 6 or 7 on *Pompeius* and less than the 10 on *Vinius*). The third segment of the palpus protrudes from the second much more than on either *Vinius* or *Pompeius*. *Vinpeius* has fine mid tibial spines only on the inner surface as *Vinius* and not stout spines on both the inner and outer surfaces as on *Pompeius*. The forewing discal cell of *Vinpeius* is shorter in relation to the anal margin than on either *Pompeius* or *Vinius* (over 80% its length on both genera). The origin of forewing vein CuA_2 is intermediate between the origin of this vein on *Pompeius* and *Vinius*. The androconial structure of *Vinpeius* extends across wing cells and thus is a stigma rather than brands which are simpler structures and parallel to veins. The species of *Vinius* obviously have brands, these in an unusual position over and under the middle of vein CuA_2 as noted by Evans (1955). The structure of the stigma on *Vin-*

peius is very different from those on the *Pompeius* species examined, being much less complex. *Vinpeius* lacks the prominent hindwing hair tuft present on *Vinius*. The genitalia of *Vinpeius* differ in several respects from both *Vinius* and *Pompeius*, especially in the form of the aedeagus.

No other genus has the combination of characters seen on *Vinpeius*; it will not key to any of the eight Hesperine group keys in Evans (1955) despite his inclusion of *V. tinga* in *Pompeius*. In the "Hesperia Group" key *V. tinga* will key to the "Phebiades Sub-group" with "Nudum of 14 or more segments." Even if it remained in the "Hesperia Sub-group" including *Pompeius*, there are not more nudum segments on the club than on the apiculus. *Vinpeius* has too many segments to the nudum to key to any "Vinius Group" genus in Evans (1955).

The relationships of *Vinpeius* are, at best, unclear. Its stigma somewhat suggests that among the genera of the last half of Evans' (1955) "Hesperia Group" taxa, its antennal structure suggests the "Vinius Group" or "Apaustus Group", and the general color and pattern is characteristic of both the "Vinius" and "Hesperia" groups. The problems with Evans' (1955) often artificial groupings have been reiterated (e.g., Burns 1990) and the previous inclusion of *V. tinga* in both *Vinius* and *Pompeius* further demonstrates these problems. For the present, placement of *Vinpeius* among the "Vinius Group" taxa should suffice.

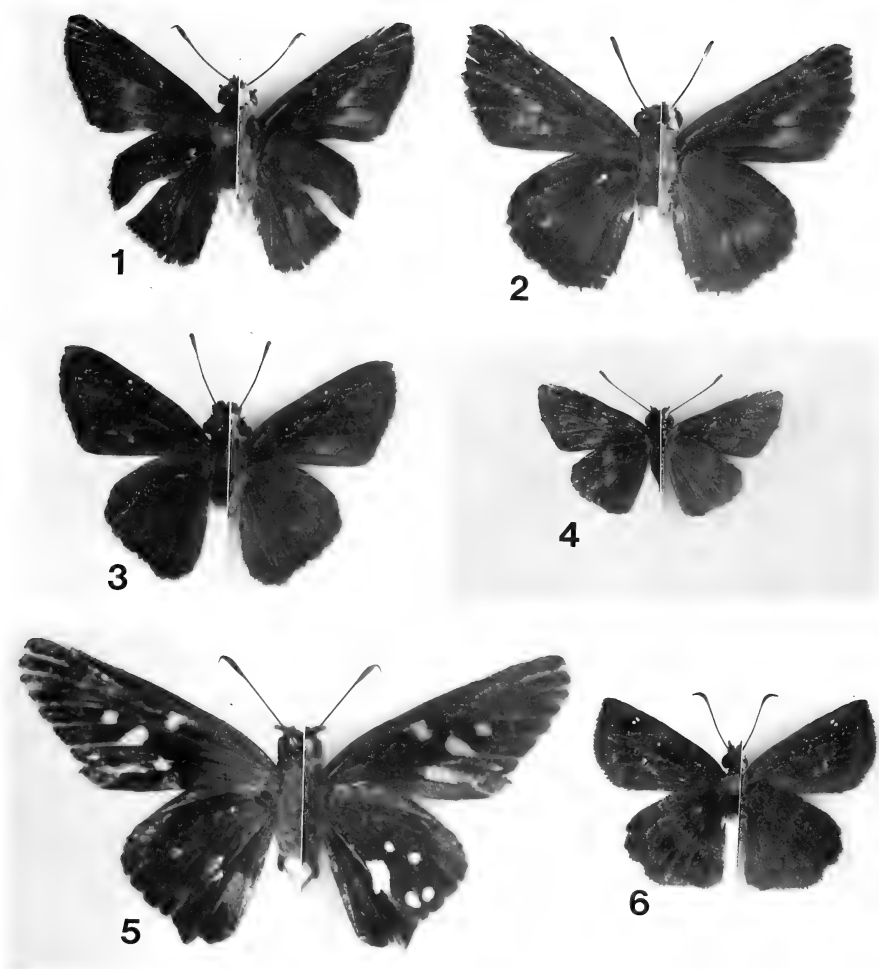
***Inglorius* Austin, new genus**

Type species: *Inglorius mediocris* Austin, new species

Description. Palpi slender, third segment straight, protruding well beyond second segment, about equal to length of dorsal edge of second segment; antennae long, extending beyond end of forewing discal cell, nearly 60% length of forewing costa, black with pale ochreous beneath distad and below club; club just over 1/4 (28%) antennal length, bent to apiculus at thickest part, apiculus length about 2× club width, nudum gray, of 12 segments (3 on club, 9 on apiculus); forewing discal cell slightly produced, 75% length of anal margin, origin of vein CuA_2 nearer to CuA_1 than to wing base, hindwing discal cell just over 1/2 wing width; mid tibiae with four fine spines on inner surface and single pair of spurs, hind tibiae with two pairs of spurs; forewing produced with slight concavity between CuA_1 and 2A; hindwing convex anteriorly, somewhat concave between CuA_1 and 2A; no apparent secondary sexual characters. Male genitalia with short tegumen; uncus longer than tegumen, undivided, and hoodlike over gnathos; gnathos as long as uncus, divided, extending laterad of uncus in dorsal view and as rectangular flaps mesad in ventral view; vinculum sinuate; saccus short; valva very long, ampulla/costa long and sloping somewhat downward caudad, harpe long, roughly triangular ending in an inward turned point caudad, dorsal margin undulate, weakly serrate cephalad; aedeagus tubular (anterior portion missing), caudal end expanded terminally in lateral view, no apparent cornutus.

Etymology. The name means "undistinguished," as the only known species of the genus is a nondescript brown insect.

Diagnosis. *Inglorius* appears to belong within Evans' (1955) "Apaustus Sub-group" of his "Apaustus Group" characterized by a long third segment of the palpi. Most of these fourteen genera contain brown species with few distinguishing marks. None of these, nor any other hesperiine, has the combination of characters seen on *Inglorius* as outlined



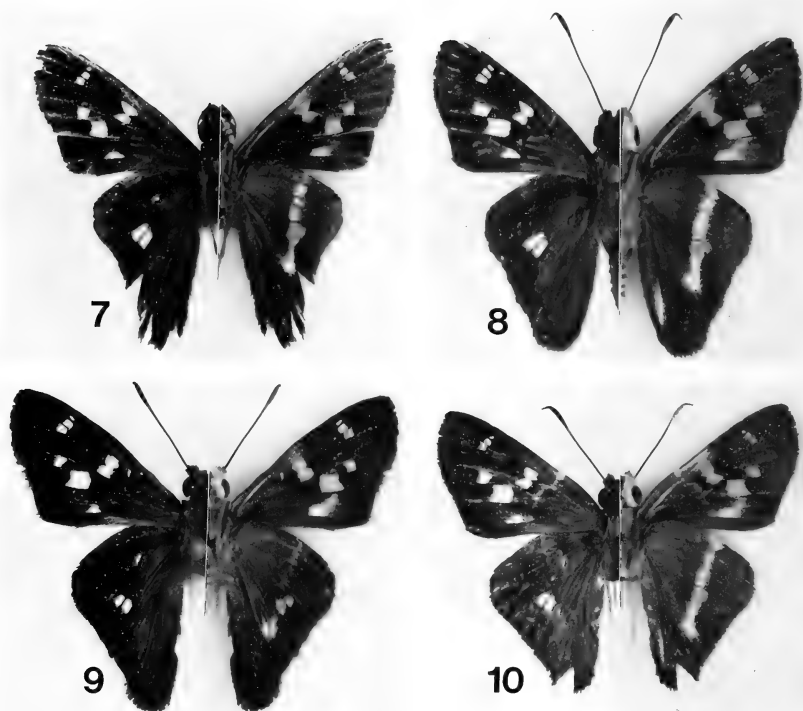
FIGS. 1-6. Hesperidae from northern Guatemala (dorsum on left, venter on right; all from GUATEMALA: Petén; Parque Nacional Tikal, unless noted otherwise). 1, *Euphyes antra*, male (25 June 1993). 2, *E. antra*, female (30 July 1992). 3, *Styriodes zeteki*, male (15 July 1993). 4, *Inglorius mediocris*, holotype male. 5, *Aides brilla*, female (29 Dec. 1992). 6, *Staphylus lenis*, female (south of Parque Nacional Tikal, east of Cauba, 1 Oct. 1994).

above. The genitalia are particularly unique and totally unlike those of any other known taxon.

***Inglorius mediocris* Austin, new species**

(Figs. 4, 12)

Description. Male: forewing length of holotype = 11.8 mm; in addition to generic description above, dorsum brown, scattered ochreous scales, these forming vague macules

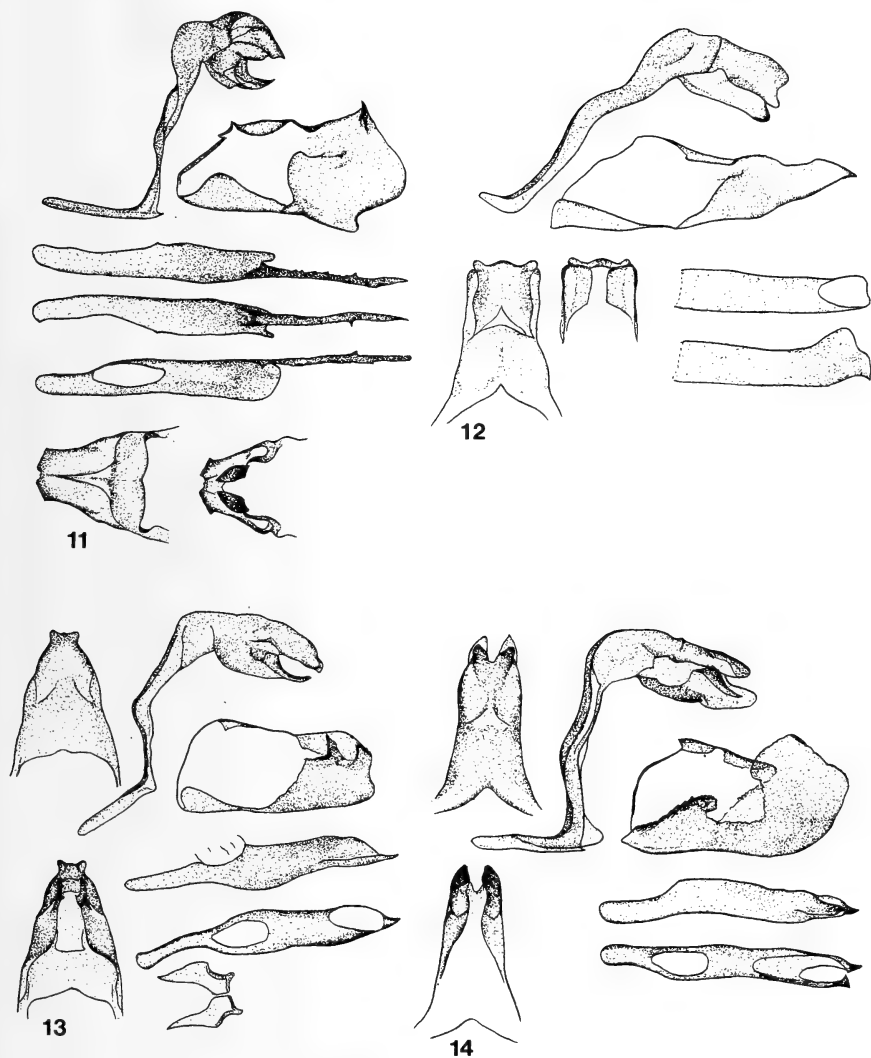


FIGS. 7–10. *Niconiades* species (dorsum on left, venter on right). 7, *N. incomptus*, holotype male. 8, *N. xanthaphes*, male (BRAZIL: Rondônia; 62 km S of Ariquemes, linha C-20, Fazenda Rancho Grande, 27 Nov. 1991). 9, *N. incomptus*, paratype female (GUATEMALA: Petén; El Remate, Cerro Cahui, 29 Sept. 1994). 10, *N. xanthaphes*, female (same location as Fig. 8, 14 Nov. 1992).

(not seen except under magnification) in CuA_1 - CuA_2 just beyond origin of CuA_1 , smaller macules offset distad in M_3 - CuA_1 and in upper portion of discal cell; long ochreous hair-like scales on forewing at base of CuA_2 -2A and along basal 1/2 of anal margin; hindwing immaculate with ochreous hairlike scales on posterior 1/2; fringes of both wings very worn, appearing gray. Ventral forewing paler brown especially distad, slight purplish cast along costa; hindwing with similar purplish cast over most of wing except for brown anal fold, small cream-colored macules at distal end of discal cell and as postmedian row from Rs to CuA_2 . Head brown with scattered ochreous scales especially around eyes; palpi gray with scattered white scales beneath becoming white and then ochreous on sides; thorax brown with scattered ochreous scales above, whitish beneath, legs pale brown; dorsal abdomen brown, ventral abdomen white (possibly with dark central line). Genitalia: see generic description above. Female: unknown.

Type. Holotype ♂ with the following labels: white, printed - Tikal, Petén / Guatemala / September 12, 1993 / D. L. Lindsley; printed and handprinted - Genitalia Vial / GTA - 5283; red, printed - HOLOTYPE / *Inglorius mediocris* / Austin. The holotype will be deposited in the Entomological Collections at the Universidad del Valle, Guatemala City, Guatemala. *Type locality.* GUATEMALA: Petén; Parque Nacional Tikal.

Etymology. The name means "ordinary" as this is a rather ordinary brown skipper.



FIGS. 11–14. Genitalia of male Hesperiidae; all from GUATEMALA: Petén. **11**, *Vinpeiusinga*, GTA Vial #5230 (lateral view of uncus, gnathos, tegumen, vinculum, saccus; internal view of right valva; right and left lateral and dorsal views of aedeagus; dorsal and ventral views of uncus, gnathos, and caudal end of tegumen). **12**, *Inglorius mediocris*, holotype, GTA Vial #5283 (lateral view of uncus, gnathos, tegumen, vinculum, saccus; internal view of right valva; dorsal and left views of caudal end of aedeagus; dorsal view of uncus, gnathos, and tegumen; ventral view of uncus and gnathos). **13**, *Mnasius nitra*, GTA Vial #3236 (lateral view of uncus, gnathos, tegumen, vinculum, saccus; internal view of right valva; left and dorsal views of aedeagus; dorsal and ventral views of uncus, gnathos, and tegumen; ventral view of juxta). **14**, *Euphyes antra*, GTA Vial #5190 (lateral view of uncus, gnathos, tegumen, vinculum, saccus; internal view of right valva; left and dorsal views of aedeagus; dorsal and ventral views of uncus, gnathos, and tegumen).

Diagnosis and discussion. The type of *Inglorius mediocris*, a worn male of a small, nearly entirely brown, skipper does not resemble any described genus or species (see also generic diagnosis above). The species is known only from the holotype taken in mid September.

Methionopsis dolor Evans, 1955

This species has previously been reported from Panama southward (Evans 1955). Single males were taken at Tikal by D. Lindsley on 11 and 12 Sept. 1993.

Mnasitheus nitra Evans, 1955

(Fig. 13)

Evans (1955) described *M. nitra* based on a pair of males from Paraná, Castro (southern Brazil). There seems to be no subsequent report of this species although it is known from Peru (*fide* O. Mielke). It thus was a surprise to find it among the Tikal area fauna. Three males, all from Parque Nacional Tikal, were taken on: 29 Feb. 1992, leg. N. M. Haddad; 31 May 1992, leg. N. M. Haddad, and 8 June 1994, leg. G. A. Orellana. The genitalia of one of these is illustrated.

Parphorus storax storax (Mabille, 1891)

Evans (1955) recorded the distribution of this species as from Costa Rica southward. Monroe and Miller (1967) reported a record for Honduras. It was not known from El Salvador (Steinhauser 1975) nor Mexico (de la Maza et al. 1991). A male from Parque Nacional Tikal taken on 4 Feb. 1992 by G. T. Austin represents a northward extension of its known distribution.

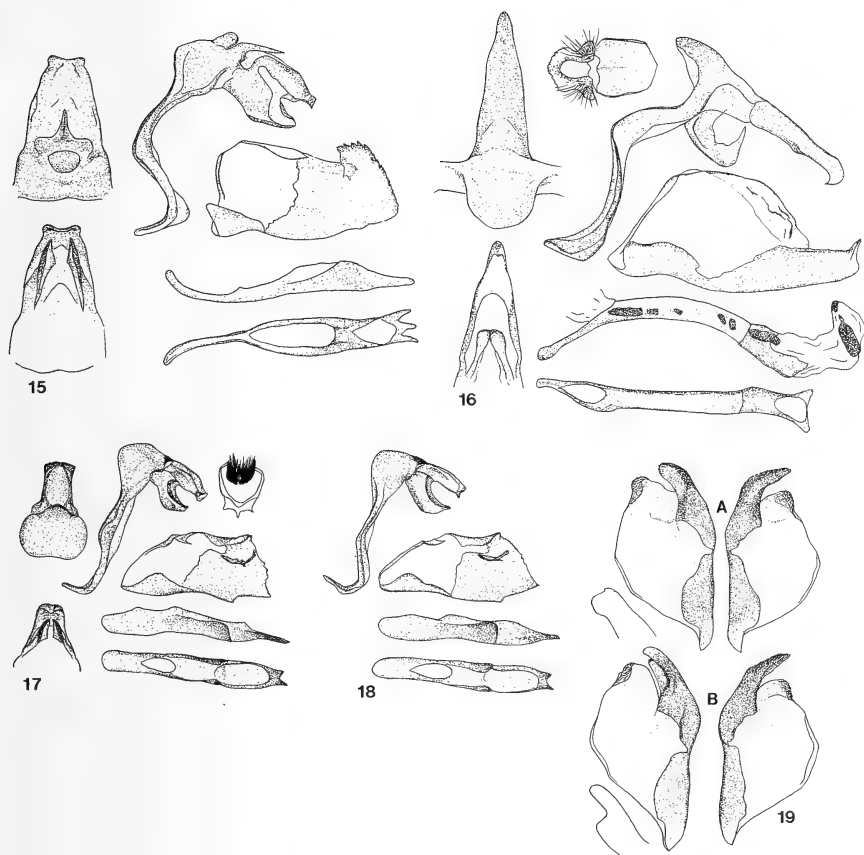
Styriodes zeteki (Bell, 1931)

(Figs. 3, 15)

This species was described from a single male taken on Barro Colorado Island in the Canal Zone, Panama (Bell 1931), not from Bolivia as stated by Evans (1955) and has not otherwise been reported. Two males from Tikal taken on 15 July 1993, leg. G. A. Orellana and 12 Sept. 1993, leg. D. Lindsley represent a considerable extension of the known distribution. The male genitalia are illustrated here in more detail than previously.

Phlebodes campo sifax Evans, 1955

This species has only been known from South America and as far north as Guyana (Evans 1955). A male from Parque Nacional Tikal taken on 31 May 1992 by N. M. Haddad represents a significant extension of the reported distribution.



FIGS 15–19. Genitalia of male Hesperidae; all from GUATEMALA: Petén, unless noted. **15**, *Styriodes zeteki*, GTA Vial #4699 (same structures as Fig. 14). **16**, *Cyclosemia leppa*, GTA Vial #1992 (same structures as Fig. 13). **17**, *Niconiades incomptus*, holotype, GTA Vial #5171 (same structures as Fig. 13). **18**, *Niconiades xanthaphes*, GTA Vial #2524 from same location as Fig. 8 (lateral view of uncus, gnathos, tegumen, vinculum, saccus; internal view of right valva; left and dorsal views of aedeagus). **19A**, *Nisoniades rubescens*, GTA Vial #5147 (internal view right and left valvae; flattened view of caudal end of right harpe). **19B**, *Nisoniades rubescens*, GTA Vial #5135 (same structures as Fig. 19A).

Euphyes antra Evans, 1955
(Figs. 1, 2, 14, 20)

This species was described based on one male from Lima, Peru, and two putative females from “Lower Amazons” (Evans 1955). Mielke (1972) found that the two females were of another taxon, *Euphyes de-rasa tuba* Evans, 1955, and knew of no other records of *E. antra*. An indication of how little we know of Neotropical hesperiid faunas was the discovery of a male and female of *E. antra* among the Tikal material

taken in the park on 25 Jan. 1993 and 30 July 1992, respectively, by G. A. Orellana. Since Mielke (1972) was unable to illustrate all the structures of the male genitalia, these are fully illustrated here. The female has not been previously described. It is similar to the male with broader and less produced wings and the pale yellow median band on the ventral hindwing is broader. The genitalia are most similar to those of Mielke's (1972) "*subferruginea*" and "*peneia*" groups with, especially, the long and relatively thin ductus bursae.

Amblyscirtes tolteca tolteca Scudder, 1872

Freeman (1993) recently reviewed the distribution of this species and indicated a distribution over most of Mexico including Chiapas. Steinhauser (1975) tentatively included this species for El Salvador but the record has not been verified. A single male from Parque Nacional Tikal taken on 14 July 1992 and two more taken on 18 July 1992 by G. A. Orellana represent a new record for Guatemala and an eastern extension of the species' distribution.

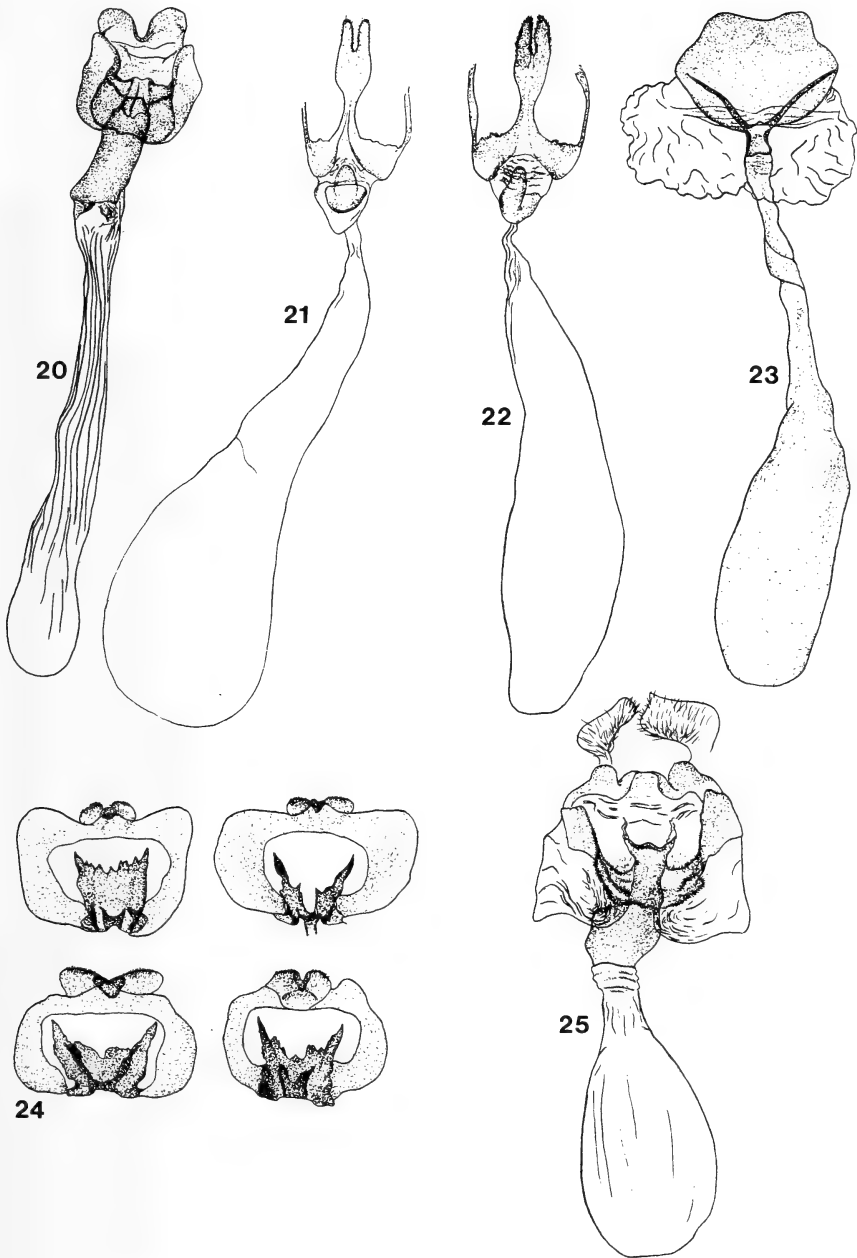
***Niconiades incomptus* Austin, new species**

(Figs. 7, 9, 17, 21)

Description. Male: forewing length = 17.1 mm (holotype), 17.0 mm (paratype); forewing produced, apex moderately rounded, termen slightly concave in $\text{CuA}_2\text{-}2\text{A}$; hindwing narrow, apex rounded, termen concave to prominently elongate tornus; dorsum blackish brown with prominent blue-green in basal 1/3 of $\text{CuA}_2\text{-}2\text{A}$ and basal 1/2 of anal margin of forewing and on basal 1/2 of hindwing; forewing with three short gray brands, one above the other, one above vein CuA_2 at base of cell (the broadest), one below CuA_2 , and another above 2A; forewing with very pale yellow hyaline macules as follows: in discal cell, strongly constricted in middle nearly separating upper and lower portions; $\text{CuA}_2\text{-}2\text{A}$, semicircular in lower half of cell over middle of vein 2A; mid $\text{CuA}_1\text{-CuA}_2$, square with slightly excavate distal edge; $\text{M}_3\text{-CuA}_1$, more or less quadrate, smaller than and offset distad from or contiguous with that in $\text{CuA}_1\text{-CuA}_2$; subapical, aligned in $\text{R}_3\text{-R}_4$, $\text{R}_4\text{-R}_5$, $\text{R}_5\text{-M}_1$, rectangular, that in $\text{R}_3\text{-R}_4$ smallest; fringe dark gray anteriorly, white behind vein CuA_2 ; hindwing with very pale yellow, more or less rectangular hyaline macules in $\text{M}_3\text{-CuA}_1$ and $\text{CuA}_1\text{-CuA}_2$; fringe brown at apex and tornus, otherwise white. Venter blackish brown, paler brown distad; forewing with macules repeated from dorsum, that in $\text{CuA}_2\text{-}2\text{A}$ more quadrate, extended, especially distad, by white scaling, elongate cream-colored macule anterior to discal cell macule in Sc-R_1 and $\text{R}_1\text{-R}_2$, this extending basad as sparse scaling to wing base in Sc-R_1 , similar scaling in base of costal cell; hindwing with hyaline macules outlined with white; narrow white band with ill-defined margins from costa (where vague) posteriad (including hyaline macules) to vein 2A where broadest and hooked somewhat basad. Dorsum of head, thorax, and anterior abdomen blue-green, posterior abdomen

→

FIGS. 20–25. Genitalia (ventral view, including lamellae, antrum, ductus bursae, corpus bursae) of female Hesperiiidae (all from GUATEMALA: Petén, unless noted). **20**, *Euphyes antra*, GTA Vial #6318. **21**, *Niconiades incomptus*, paratype, GTA Vial #5172. **22**, *Niconiades xanthaphes*, GTA Vial #3128, from BRAZIL: Rondônia. **23**, *Ridens allyni*, GTA Vial #5281. **24**, *Staphylus lenis*, GTA Vial #5298, #5290, #5300, #5301 (lamellae). **25**, *Aides brilla*, GTA Vial #5282 (including papillae anales).



dark brown; palpi blue-green above, whitish beneath and on cheeks; antenna black, vaguely white at base of club beneath, nudum dark gray with 17, 18 segments; pectus bright ochreous with green tinge; legs dark brown with some pale ochreous scaling, mid tibiae spined and with single pair of spurs, hind tibiae with two pairs of spurs; ventral abdomen whitish with very broad black median band. Genitalia: tegumen bulbous; uncus undivided, broad, blunt; gnathos slightly shorter than uncus, divided, pointed caudad, arms somewhat convergent; vinculum slightly sinuate; saccus short, upturned; valva broad, harpe stout, triangular, dorso-caudal margin with irregular fine serrations, produced to short tooth just after ampulla, ventral margin narrowly excavate, prominent "shelf" protruding mesad from upper inner surface; juxta as narrow band, ventral portion trifurcate cephalad, large cluster of bristles dorsad; aedeagus tubular, narrowing caudad to lateral prongs ventrad, left prong slightly longer than right; no cornutus. Female: forewing length 17.0, 18.8, 19.8 mm; similar to male; no brands; forewing discal cell macule less constricted in middle; forewing broader; hindwing termen less concave; antennal nudum with 18, 18, 19 segments. Genitalia: lamella postvaginalis not well developed; lamella antevaginalis with long central process extended caudad where bifurcate; ductus bursae and corpus bursae not clearly separable, gradually expanding to bulbous cephalad end.

Types. Holotype ♂ with the following labels: white, printed - GUATEMALA / Petén, El Remate / Cerro Cahui / 30 Sept. 1994 / leg. G. T. Austin; white, printed and hand-printed - Genitalia Vial / GTA - 5171; red, printed - HOLOTYPE / *Niconiades incomptus* / Austin. Paratypes - same location as holotype, 29 Sept. 1994, leg. G. A. Orellana (1 ♂); 28 Sept. 1994, leg. G. T. Austin (1 ♀); 29 Sept. 1994, leg. G. T. Austin (1 ♀); Parque Nacional Tikal, 25 Mar. 1992, leg. N. M. Haddad (1 ♀); 26 Sept. 1992, leg. J. V. Orellana (1 ♀). The holotype and a female paratype will be deposited in the Entomological Collections at the Universidad del Valle, Guatemala City, Guatemala. *Type locality.* GUATEMALA: Petén; El Remate, Cerro Cahui. This is on the north shore of Lago Petén Itza with a mosaic of mature and second growth forests. Most of the types were taken along the forest edge.

Etymology. The name means "untrimmed" referring to the ventral hindwing white band without well-defined edges.

Distribution. The distribution of this species is currently unknown and some of the *Niconiades xanthaphes* Hübner, [1821] reported from Central America and elsewhere may refer to *N. incomptus*. A pair of *N. incomptus* was seen from the Atlantic Slope of Costa Rica (male from Limon Province, female from Heredia Province); another pair was seen from the vicinity of Candelaria, Oaxaca, Mexico. All reports of *N. xanthaphes* from Mexico south through Central America should be treated as suspect until the specimens are reexamined. Certainly, *N. incomptus* is more widespread than the records indicated above and is residing in collections among series of *N. xanthaphes*.

Diagnosis and discussion. This new species is most similar to *N. xanthaphes* which may be slightly smaller in size (male forewing length = 16.7 mm [15.9–17.9, $n = 10$], female forewing length = 16.6, 17.3, samples from Rondônia, Brazil). The forewing of *N. xanthaphes* (Figs. 8, 10) is stouter and less produced apically than on *N. incomptus* (Figs. 7, 9), the hindwing is broader and less concave with a shorter anal lobe, the ventral forewing has the macules anterior to the discal cell macule more distinct and pale yellow-orange, the hindwing band is broader, nearly the full width of the hyaline macules, and with margins sharply defined, and there is a narrow white streak along the distal 1/3 to 1/2 of vein 3A.

While *N. incomptus* is readily separable from *N. xanthaphes* by characters of the wings (Figs. 7–10), the genitalia of the two species are very similar. The male genitalia of *N. incomptus* do not appear separable from those of *N. xanthaphes* (Fig. 18); those illustrated by Godman and Salvin (1879–1901), Hayward (1951), and Evans (1955) could be of either species. The female genitalia are also very similar but the central process of the lamella antevaginalis on *N. incomptus* is less robust than on *N. xanthaphes* (Fig. 22). The forewing with brands illustrated by Godman and Salvin (1879–1901) appears to be *N. xanthaphes* based upon the more rounded and less produced apex; they may have seen both species as there is no mention of the white streak on the anal margin of the ventral hindwing. Hayward (1951) mentioned this character and undoubtedly saw *N. xanthaphes* from Argentina. Mielke (pers. comm.), in review of this manuscript, suggested that *N. incomptus*

tus was a northern subspecies of *N. xanthaphes*, but he indicated overlap between the two in Panama.

Aides brilla (Freeman, 1970)

(Figs. 5, 25)

A male from Tikal (16 Sept. 1993, leg. N. M. Haddad) is like the single previously reported specimen, the holotype male from Catemaco, Veracruz, Mexico (Freeman 1970). An additional *Aides* from Tikal (29 Dec. 1992, leg. G. A. Orellana) is apparently the first known female *A. brilla*. The wings are more elongate than on the male (forewing length = 26.5 mm) and the dorsal color and pattern is virtually identical except the discal cell macule is further from the macule in $\text{CuA}_1\text{-CuA}_2$. The ventral forewing is similar to that of the male as is the color of the ventral hindwing. The silverly-white maculation of the ventral hindwing, however, differs. The large macule in $\text{CuA}_2\text{-2A}$ is similar in shape but does not extend as far basad, there is no macule in the base of $\text{CuA}_1\text{-CuA}_2$, the discal cell macule is a small round spot, similar (slightly larger) spots occur in the middle of $\text{M}_1\text{-M}_3$ and submargin of $\text{M}_3\text{-CuA}_1$, and an additional oval macule is in the submargin of $\text{CuA}_1\text{-CuA}_2$. The genitalia of this female are illustrated.

PYRGINAE

Ridens allyni Freeman, 1979

(Fig. 23)

This species is known from Veracruz, Oaxaca, and Chiapas, Mexico (Freeman 1979). It is not uncommon in the Tikal region with records for 11 Mar. 1993, leg. G. A. Orellana (1 male), 13 July 1992, leg. G. A. Orellana (1 female), 18 July 1992, leg. G. A. Orellana (1 male), 23 Aug. 1993, leg. J. V. Orellana (1 female), and 25 Sept. 1992, leg. G. A. Orellana (1 male). The female genitalia are illustrated for the first time herein.

Nisoniades rubescens (Möschler, [1877])

(Fig. 19)

Eight male *Nisoniades* Hübner, 1819 from Tikal were identified as *N. rubescens* with the key in Evans (1953). These, however, exhibit two somewhat different configurations of the valvae, especially the right. One phenotype, represented by a single specimen (Fig. 19A), is that illustrated as *N. rubescens* by Evans (1953) or its putative synonym *Pellicia bromias* Godman & Salvin, [1894] illustrated by Godman & Salvin (1879–1901) and Hayward (1948). On this, the ampulla/costa of the right valva is broadly and evenly convex, the caudal end of the ampulla has a somewhat upward orientation, and the harpe is broadly rounded caudad. The harpe of the left valva is rather sharply bent. The remaining

seven individuals are of the second phenotype (Fig. 19B) and has not been previously illustrated. The costa/ampulla of the right valva is less evenly convex, the caudal end of the ampulla has more of a ventrad orientation, and the caudal end of the harpe is truncated to a long and narrow finger-like lobe. The harpe of the left valva is less sharply bent.

No superficial differences between the two could be detected. Both genitalic phenotypes have also been seen among specimens from Costa Rica. Examination of additional material (including females) and of the types of *N. rubescens* and its listed synonyms *P. bromias*, *Pellicia clara* Mabille & Boulet, [1917], *Pellicia nigra* Mabille & Boulet, [1917], and *Achlyodes triangulus* Mabille, 1897 are required to properly evaluate the observed variation; two species may be involved. Evans (1953) noted variation in the genitalia of *Nisoniades maura* (Mabille & Boulet, [1917]), *Nisoniades mimas* (Cramer, [1775]), and *Nisoniades ephora* (Herrich-Schäffer, 1870).

Cyclosemia leppa Evans, 1953

(Fig. 16)

This species is evidently known only from the holotype male from Bolivia and a female from Peru (Evans 1953). A single very worn male taken at Tikal on 4 Feb. 1992 by G. T. Austin represents a major range extension. Its genitalia are illustrated herein.

Staphylus lenis Steinhauser, 1989

(Figs. 6, 24)

This species is relatively common in the Tikal region with records for February and May through October. At the time of its description, *S. lenis* was known only from males taken in Quintana Roo, Mexico and in Trinidad (Steinhauser 1989). The female (forewing length = 12.4 mm [11.7–12.8 mm, N = 4]) is similar to females of other species of the *Staphylus mazans* (Reakirt, [1867]) group, especially *Staphylus ascalaphus* (Staudinger, 1875) and *Staphylus unicornis* Steinhauser and Austin, 1993. It differs from female *S. ascalaphus* (forewing length from Costa Rica = 12.9 mm [12.2–13.3 mm, N = 10]) by its smaller mean size and less prominent contrast between the brown ground color and the blackish bands on the dorsum. It differs from the slightly larger female *S. unicornis* (forewing length from Costa Rica = 12.7 mm [12.0–13.9 mm, N = 12]) by the absence of the lower hyaline macule in the forewing discal cell (this present on most *S. unicornis*). Two of four females of *S. lenis* lack a white macule in M_3-CuA_1 ; this is absent on most *S. ascalaphus* but present on nearly all *S. unicornis*.

The lamellae of the female genitalia of *S. lenis* are highly variable (Fig. 24) as also shown for *S. ascalaphus* and *S. unicornis* by Steinhauser

(1989) and Steinhauser and Austin (1993). Generally, the plate-like lamella postvaginalis of *S. lenis* has a roughly heart-shaped and heavily sclerotized central process (this varies in size and shape) on its caudal edge, flanked by usually oval membranous lobes (also variable in size) with microtrichia especially caudad. The lamella antevaginalis has a caudally excavate central plate with two large and caudally pointed lateral processes and central serrations; the depth of the central concavity and number of serrations varies. No other *S. mazans* group species examined have the prominent lateral processes of the lamella antevaginalis seen on *S. lenis* (Steinhauser 1989, Steinhauser & Austin 1993).

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LIFE HISTORY AND BEHAVIOR OF *SYNAXIS CERVINARIA*
(GEOMETRIDAE), A DEFOLIATOR OF *ARCTOSTAPHYLOS*
PATULA (ERICACEAE)

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ABSTRACT. The life stages and behavior of *Synaxis cervinaria* are described from laboratory and field studies conducted in Shasta Co., California, using greenleaf manzanita, *Arctostaphylos patula*, as a host plant. Instars 1 and 2 resemble the green surface and red edges of the expanding leaves, and third instars begin to resemble twigs. The first three instars remain in the crown during the day. Instars 4 and 5 resemble twigs and stems, maintaining stick-like resting positions near the main stem below the crown during the day. The pupae overwinter. Adults emerge in late spring/early summer and oviposition occurs prior to and during manzanita leaf expansion. There is one generation per year.

Additional key words: greenleaf manzanita, crypsis, flight period, leaf consumption.

Synaxis cervinaria (Packard) (Geometridae) was described from an adult male collected in West Springs, California (Packard 1871). McGuffin (1987) described the adult female and genitalia of both sexes but noted that the egg, early larval instars, and pupa were unknown: a description based on a single preserved specimen of a "mature" larva (presumably fifth instar) was given. *Synaxis cervinaria* ranges from British Columbia south to California, and the reported hosts include: Oregon white oak, *Quercus garryana* Hooker (Fagaceae) (Jones 1951); an unidentified *Quercus*; poplar, *Populus* sp. (Populaceae) (McFarland 1965); *Arbutus* (Ericaceae) (McGuffin 1987); willow (Salicaceae); bitterbrush (Rosaceae); cascara and species of *Ceanothus* (Rhamnaceae) (Miller 1995).

In 1990, as part of a broader study of the insect fauna associated with *Arctostaphylos patula* E. Greene (Ericaceae) (Valenti 1994), we found larvae of *S. cervinaria* on this plant near Hat Creek, Shasta Co., California. This manzanita commonly occurs throughout the western United States in montane forest zones (Ball et al. 1983) and is of concern to forest land managers because it often inhibits the survival, regeneration, and growth of conifers (Radosevich 1984). In response to a general lack of information regarding insect fauna associated with chaparral commu-

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nities (Force 1990), especially species of manzanita (Haws et al. 1988), we conducted a study of *S. cervinaria* and its interactions with greenleaf manzanita.

This paper presents life history and behavioral information for *S. cervinaria*, one of six geometrids encountered during our faunal survey (Valenti & Zack 1995) that utilizes greenleaf manzanita as a host plant. The goals of this study were to: 1) determine adult flight period; 2) describe larval stages and behavior and determine stadium lengths; 3) measure leaf consumption of *A. patula* by larvae; 4) establish a list of acceptable foodplants associated with greenleaf manzanita communities in the Hat Creek area; and 5) identify natural enemies of eggs and larvae.

MATERIALS AND METHODS

Synaxis cervinaria laboratory studies, rearings, and adult collections were conducted at the Forest Insect Laboratory, USDA Forest Service, Hat Creek, California. Field studies were conducted at two sites in Shasta Co., California. The first site was adjacent to the USDA Forest Service Work Center at Hat Creek (T34N R4E S16) (elev. 1018 m) and contained a variety of woody plant species. Greenleaf manzanita accounted for less than 30% (canopy coverage) of the total vegetation. Other common plants included: sagebrush (*Artemesia tridentata* Nuttall) (Compositae), curl-leaf mountain-mahogany (*Cercocarpus ledifolius* Nuttall), birch-leaf mountain-mahogany (*C. betuloides* Torrey & A. Gray), antelope bitterbrush (*Purshia tridentata* [Pursh] de Candolle) (Rosaceae), California black oak (*Quercus kelloggii* Newberry) (Fagaceae), ponderosa pine (*Pinus ponderosa* Lawson), sugar pine (*P. lambertiana* Douglas), white fir (*Abies concolor* [Gordon & Glendinning] Lindley), Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco), incense cedar (*Calocedrus decurrens* [Torrey] Florin), and western juniper (*Juniperus occidentalis* Hooker) (Pinaceae). The second site (elev. 1512 m) was 3.2 km northwest of California Route 89 near Logan Lake in Old Station, ca. 24 km south of Hat Creek (T32N R4E S2&3). Dominant vegetation (canopy coverage) consisted of greenleaf manzanita (74%), tobacco brush (11%), *Ceanothus velutinus* Hooker (Rhamnaceae), and ponderosa pine (9%). This 50+ ha site is on an east-facing slope and was mechanically cleared of all vegetation in 1976 and planted with ponderosa pine in 1977.

During 1991 and 1992, a 15 watt black light was used at the Hat Creek Forest Insect Laboratory to determine the flight period of *S. cervinaria*. All adults collected from 2100–2300 h each evening were tallied, a portion of the males was retained as vouchers, and most females were placed in covered 236 ml plastic cups for egg collection. Be-

havioral data, including egg-laying, were obtained by observing adults in the field and in screen cages ($45 \times 45 \times 75$ cm).

Larval rearing containers were constructed from clear plastic cylindrical tennis ball containers 20 cm in height and 7 cm in diameter. A single neonate larva was placed on a greenleaf manzanita branch in each of 30 containers. Larval development under ambient conditions was observed daily until pupation. Foliage was replaced once, following the fourth instar molt. Frass of the first four instars was collected from the bottom of each rearing container when foliage was changed, and again after pupation. All leaves damaged by the fifth instars were collected, pressed, mounted to sheets of standard card stock, and missing portions of each leaf were drawn freehand. A digitizer was then used to measure leaf area consumed (cm^2). Frass weight was used to estimate leaf area consumption for first through fourth instars. Head capsule widths and total body lengths of 30 individuals in each instar (reared in $45 \times 45 \times 75$ cm cages) were measured to the nearest 0.05 mm using an ocular micrometer.

A host suitability study was conducted by placing 15–40 unfed first instars onto foliage from various plants in the families Pinaceae, Compositae, Ericaceae, Fagaceae, Rhamnaceae, and Rosaceae. Observations were made daily to determine if larvae were feeding and continuing to develop. This procedure was repeated for a group of fourth instars that had previously fed on greenleaf manzanita foliage.

One day old egg masses collected from captured females were placed in the field. Prior to larval eclosion (ca. 10 days), egg masses were collected and transferred to Petri dishes. Adult parasitoids that emerged from eggs were collected and preserved. Larvae from a laboratory colony were periodically placed onto greenleaf manzanita branches in the field; those recovered several days later were reared individually to obtain parasitoids.

Statistix© was used to perform all statistical analyses (Siegel 1992), following methods of Steel & Torrie (1980). Representative voucher specimens of all taxa have been deposited in the Maurice T. James Entomological Collection at the Department of Entomology, Washington State University, Pullman, Washington.

LIFE HISTORY

Adult. Adult *S. cervinaria* flew at Hat Creek from early June to late July in 1991 and mid-May to late June in 1992 (Fig. 1). Adults have historically been collected in April, May, and June (Jones 1951), and early July (one specimen in the Essig Museum of Entomology, University of California Berkeley). Thus, based on these collection records and our data there appears to be one generation per year.

During 1991, 160 males and 166 females were collected giving a capture sex ratio of nearly 1:1. In 1992, 102 males and 114 females were collected (1.0:1.1 ratio). Adults survived up to 11 days in captivity. More than 94% of captured females produced eggs. All egg-producing females were fertile. Many *S. cervinaria* females attracted to the black light

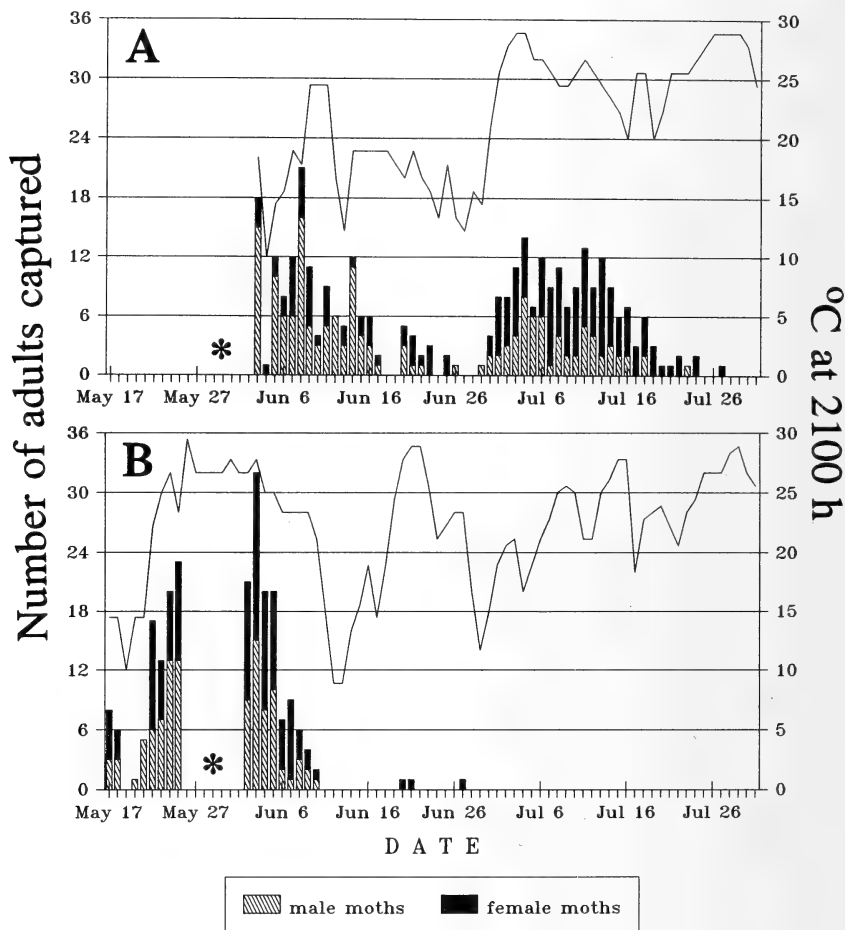


FIG. 1. Flight period of *Synaxis cervinaria* in 1991 (A) and 1992 (B). All adults attracted to a 15 watt black light were collected nightly from 2100–2300 h at the Forest Insect Laboratory, USDA Forest Service, Hat Creek, California. Asterisks indicate adults not collected before 2 June 1991 nor between 26 May and 1 June 1992.

showed little or no sign of wear (Fig. 2A), and had likely emerged within a few days of capture. Virgin females placed in screen cages with adult males for 24 h produced viable eggs. These observations strongly suggest mating occurs soon after emergence from overwintering pupae. Although mating in the field or laboratory was never observed, adults of at least some other geometrid species (e.g., *Stannodes animata* [Pearsall]) are known to mate prior to flight (Furniss et al. 1988). An adult female collected in 1989 had seven spermatophores within her bursa (K. Bolte, pers. comm.).

Female *S. cervinaria* use their papillae anales to locate a leaf edge. Eggs are deposited along the leaf edge, in a single row of several to about 30 (Fig. 2B). Under cramped artificial conditions egg deposition also occurred along the edges of any available substrate (container lids, folded wax paper, cage frames, etc.), and they were often layered two or three deep. Eggs were always oriented with the micropylar end near the substrate edge.

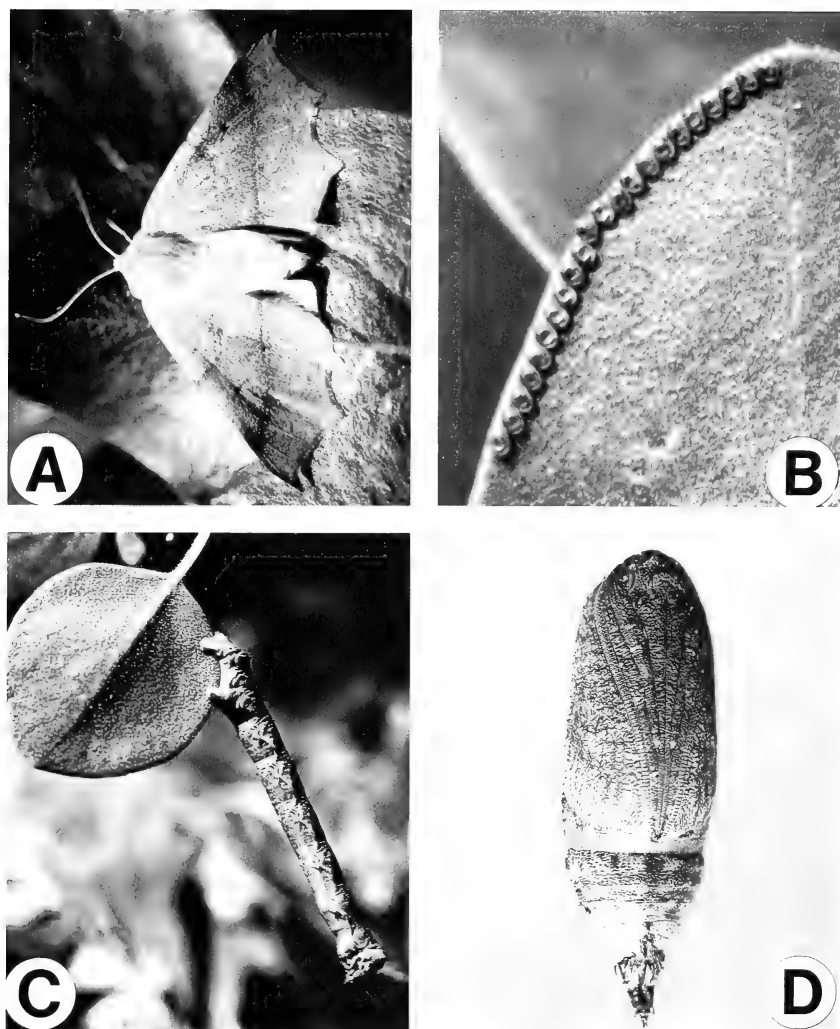


FIG. 2. *Synaxis cervinaria* life stages. A, adult female. B, typical egg mass along leaf edge. C, fifth instar in a typical resting position on a greenleaf manzanita leaf. D, female pupa.

Several egg masses were encountered in the field on greenleaf manzanita leaves and one egg mass was collected from a tobacco brush leaf at the Logan Lake site.

More than 90% of the eggs produced by females in captivity were deposited after 2100 h over a period of three or four nights. In 1991 a total of 159 captured females produced 11,474 eggs for an average of 72 eggs per female (range: 0–230). In 1992, 94 captured females produced 5207 eggs for an average of 55 eggs per female (range: 0–139). Some of these females may have deposited a portion of their eggs before flying to the black light. From a sample of 2110 eggs deposited by 30 females, 1846 produced larvae (87.5% hatching rate).

TABLE 1. Host suitability tests for *Synaxis cervinaria* larvae. No indicates that larvae do not feed and eventually starve to death; yes indicates that larvae feed and continue to grow and develop.

Host family/species	Feeding/frass
Pinaceae	
<i>Abies concolor</i> (white fir)	no
<i>Calocedrus decurrens</i> (incense cedar)	no
<i>Juniperus occidentalis</i> (western juniper)	no
<i>Pinus lambertiana</i> (sugar pine)	no
<i>P. ponderosa</i> (ponderosa pine)	no
<i>Pseudotsuga menziesii</i> (Douglas-fir)	no
Compositae	
<i>Artemesia tridentata</i> (sagebrush)	no
<i>Chrysothamnus viscidiflorus</i> (yellow rabbitbrush)	no
Ericaceae	
<i>Arctostaphylos patula</i> (greenleaf manzanita)	yes
Fagaceae	
<i>Chrysolepis sempervirens</i> (bush chinquapin)	yes
<i>Quercus kelloggii</i> (California black oak)	yes
Rhamnaceae	
<i>Ceanothus cordulatus</i> (mountain whitethorn)	yes
<i>C. integririmus</i> (deer brush)	yes
<i>C. velutinus</i> (tobacco brush)	yes
Rosaceae	
<i>Cercocarpus betuloides</i> (birch-leaf mountain-mahogany)	yes
<i>C. ledifolius</i> (curl-leaf mountain-mahogany)	yes
<i>Prunus emarginata</i> (bitter cherry)	yes
<i>Purshia tridentata</i> (antelope bitterbrush)	yes

Egg. Smooth, somewhat oblong (0.75 mm wide by 0.95 mm long) and remaining a pale yellowish-green for ca. 24 h following deposition. The eggs begin to turn a pinkish-rose color and then crimson after a second 24 h period (eggs that remain yellow are inviable). About 12 h before hatch, the developing larva becomes visible through a translucent chorion, giving the eggs an overall reddish-gray appearance. Eggs hatch in 7–10 days depending on temperature. Parasitized eggs turn black prior to emergence of adult parasitoids.

First instar. Head capsule width (HCW) 0.45 ± 0.02 mm, total body length (TBL) 2.8–6.9 mm, stadium length (SL) 5 days (range: 4–7 days). Head capsule uniformly light brown; crimson dorsal and ventral stripes from pronotum to A9 dorsally, through A5 ventrally, otherwise translucent until feeding commences, whereupon these areas take on a greenish hue; body lacks protuberances.

Second instar. HCW 0.74 ± 0.03 mm, TBL 6.1–13.3 mm, SL 6 days (range: 5–8 days). Head capsule light brown with three sets of herring-bone patterns, more black than brown; crimson ventral region from cervix to A6 (first pair of prolegs); dorsum and lateral areas greenish-yellow due to food plant material visible through translucent integument; body lacks protuberances.

Third instar. HCW 1.19 ± 0.07 mm, TBL 11.9–21.1 mm, SL 6 days (range: 4–8 days). Head capsule with more pronounced brown herring-bone pattern; fleshy dorsolateral lobes begin to appear on the metathoracic segment late in this stadium; body color varies to some extent; mottled black, brown, and crimson dorsally; ventrally and laterally an array of colors are exhibited including white, yellow, gray, brick red, crimson, brown, and black.

Fourth instar. HCW 1.91 ± 0.10 mm, TBL 18.2–25.5 mm, SL 8 days (range: 5–13 days). Head capsule mottled/stippled brown, crimson, and white; fleshy tubercle at apex

TABLE 2. Greenleaf manzanita leaf consumption by *Synaxis cervinaria* larvae (n = 30). Total number leaves consumed determined by measuring the area of 528 mature leaves from 30 greenleaf manzanita branches to calculate a mean leaf area value ($5.32 \pm 1.69 \text{ cm}^2/\text{leaf}$).

	1st–4th Instars		5th Instar		Percent of total foliage consumed		Total number leaves consumed
	Frass wt. (mg)	Leaf area consumed (cm ²)	Frass wt. (mg)	Leaf area consumed (cm ²)	1st–4th Instars	5th Instar	
Mean	131	8.47	743	47.17	15.2	84.8	10.45
SE	16	1.82	13	6.60	2.2	2.2	1.82

of clypeus; dorsolateral metathoracic fleshy lobes more pronounced; A4, A5, and A8 dorsally with prominent paired chalazae; paired, dark colored ventrolateral and lighter colored ventromedial chalazae on A1; body coloration varies from crimson red to mottled gray with whitish hourglass patterns dorsally. These color variations are similar to those observed in both live and dead greenleaf manzanita twigs and branch stubs.

Fifth instar. HCW $2.83 \pm 0.10 \text{ mm}$, TBL $24.3\text{--}35.2 \text{ mm}$, SL 14 days (range: 9–21 days). Head capsule mottled/stippled light to dark brown, crimson, and white; fleshy tubercle at apex of clypeus; dorsolateral metathoracic fleshy lobes less pronounced; A4, A5, and A8 with prominent, paired chalazae dorsally, paired dark colored ventrolateral and lighter colored ventromedial chalazae on A1; body coloration and color patterns, as in instar four, extremely variable. Stem/twig mimicry by cryptic morphology and behavior are pronounced in the fifth instar (Fig. 2C).

Pupa. Obtect, mottled brown or tan, about 5 mm at the widest point and up to 19 mm in length. Female genitalia span the 8th and 9th abdominal segments (Fig. 2D) whereas the male genitalia on the 9th segment only has a raised longitudinal border. Pupation occurs in leaf litter below host plants.

BIOLOGICAL NOTES

Larval behavior. Larvae developed normally on a variety of woody plants, but not on conifers or composites in the feeding trials (Table 1). Feeding tests on greenleaf manzanita showed that larvae (n = 30) consumed, on average, a total of $55.64 \pm 7.48 \text{ cm}^2$ of foliage or 10.45 ± 1.82 expanded leaves (Table 2).

Neonate larvae emerge from eggs by using their mandibles to chew along a visible circular suture on the micropylar end of the egg, leaving a whitish-translucent shell with an apical exit hole. No parts of the chorion are consumed. There was no evidence of cannibalism for this or any subsequent instar, even under crowded conditions with no available food. Early instars feed by grazing the outer layers of cells from old and new foliage (greenleaf manzanita is a broadleaf evergreen that retains its leaves for more than one year), and although new foliage is preferred, larvae can develop normally on old foliage. Larval activity in late spring coincided with greenleaf manzanita leaf expansion. At the Logan Lake site, leaves first began to expand between 14–21 June in 1991 and 1–5 June in 1992, about 10 days later than at Hat Creek (494 m lower in elevation) where adults were surveyed.

First instars released onto greenleaf manzanita branches in the field usually remained on or close to (within 15 cm) the leaf on which they were originally placed. Occasionally a larva would be found on a lower stem, possibly forced from an upper branch after disturbance by wind or predator. Unidentified species of ants (Formicidae) were ubiquitous and occasionally approached larvae which then dropped from their perch on a silken thread. Eight such encounters were observed in the field but none resulted in captured larvae.

Prior to the first molt, the ventral area remains crimson but the dorsal stripe degenerates, and the dorsum and lateral areas become greenish-yellow. Laboratory-reared larvae were often observed in the evening suspended from silken threads (1.5–2.5 cm) or maintaining a characteristic stick-like appearance on the edge of a leaf (typical resting posture). The body is held in a straight and stiff position at a 30–45° angle to the substrate (usually a leaf or branch) to which the prolegs are attached, always with a silk thread from the head to an attachment site on the substrate. Larval feeding was observed both day and night.

Second instars feed by grazing on leaf surfaces and occasionally create a small hole in maturing leaves. Newly expanding leaves are sometimes consumed by feeding along the leaf edge. Larvae released in the field tended to remain on or near the point of placement if left undisturbed, similar to behavior observed for first instars.

Third instars released in the field begin to move about on the foliage, more so than the first and second instars, but they still remain relatively close to the point of release. A stick-like resting posture is maintained on or near foliage. Feeding usually occurs along leaf edges and whole leaf sections are removed.

The significance of cryptic coloration in the first three instars is not well understood. They are exposed in the canopy and presumably would be vulnerable to bird predation. However, field enclosure experiments revealed that birds had no significant effect on the survival of instars 1–3 (Valenti 1994).

Stem mimicry and crypsis in the fourth instars is made possible by a combination of resting posture, morphology, and coloration. During the day, larvae in this stadium begin to move down and away from the crown. Typically, fourth instars released in the field would be found in a 30–45° resting posture on a main stem below the crown. Larvae at this stage can consume entire leaves and feed nocturnally.

The molt to the fifth instar begins with the late fourth instar terminating its feeding and hanging by the prolegs with its head downward for several hours (the process described here is similar for the other instars). The cuticle splits at the vertex and the old head capsule is sloughed off by the thoracic legs. With undulating body movements, the

old skin is forced up towards the prolegs. Once the exuvium is slipped over the first pair of prolegs (A6) the larva transfers its anterior end back up to the leaf or branch, secures a perch with the thoracic legs, and then slips its posterior end out of the remaining old cuticle. The prolegs are then firmly attached to the branch along with a silk thread near the head. Once initiated, the entire molting period lasts about five minutes. The larva maintains itself in a typical motionless, stick-like appearance while it hardens and darkens. The shriveled exuvium remains attached to the branch, often long after molting is complete.

Fifth instars account for ca. 36% of the entire larval developmental period and inflict the most damage to greenleaf manzanita foliage (85% of the total amount of foliage consumed) (Table 2). They feed at night on entire leaves and remain in the lower crown or near the plant base during the day.

Fourth and fifth instars avoid detection by visually searching predators (e.g., birds) by resting during the day below the crown. Their resemblance to stems and twigs and their resting posture make them very difficult to detect. Although we never observed significant defoliation in the field and there have been no outbreaks of *S. cervinaria* reported in the literature, caged larvae completely defoliated greenleaf manzanita plants, suggesting that this geometrid is strongly regulated at low densities by natural enemies. Exclosure experiments in the field supported this supposition; in the absence of birds and ants larval survival increased nearly five-fold (Valenti 1994).

Pupae. The fifth instar drops or crawls to the ground and burrows one to two cm beneath the leaf litter surface where it spins a loose cocoon attached to pieces of litter and detritus. After 4 days (range: 3–7 days) the molting period is complete and a hardened and darkened pupa is formed. The pupa overwinters. The average weight of 30 pupae was 233 ± 22 mg. Adults emerged from pupae cold treated at 4°C for 90–120 days.

Natural enemies. Two species of wasps were reared from parasitized *S. cervinaria* eggs: *Trichogramma* sp. (Hymenoptera: Trichogrammatidae) and *Telenomus alsophilae* Viereck (Hymenoptera: Scelionidae). Individual parasitized *S. cervinaria* eggs produced two to five individuals of *Trichogramma* sp. or a single individual of *Telenomus alsophilae*.

Several parasitoids were reared from *S. cervinaria* larvae (instars attacked are in parentheses): *Campylochaeta* sp. (Diptera: Tachinidae) (4,5), *Aleiodes* n. sp. (Hymenoptera: Braconidae) (3), *Meteorus rubens* (Nees) (Hymenoptera: Braconidae) (1–5), *Dusona nigriritibialis* (Viereck) (Hymenoptera: Ichneumonidae) (3–5), *Euplectrus* sp. poss. *plathy-penae* Howard (Hymenoptera: Eulophidae) (1–5).

In the field, a female *Goniozus gracilicornis* (Kieffer) (Hymenoptera: Bethyilidae) was observed dragging a moribund third instar of *S. cervinaria* across a greenleaf manzanita leaf. It is unknown if it had paralyzed the larva. On three occasions spiders were observed successfully attacking *S. cervinaria* larvae. These were *Misumenops celer* (Hentz) (Araneae: Thomisidae), *Xysticus* sp. (Araneae: Thomisidae), and *Metaphidippus* sp. (Araneae: Salticidae).

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REVIEW OF THE NEW WORLD BAGISARINAE WITH DESCRIPTION OF TWO NEW SPECIES FROM THE SOUTHERN UNITED STATES (NOCTUIDAE)

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ABSTRACT. The Bagisarinae are discussed and characterized, including the Old World genus *Xanthodes* Guenée, 1852, which is considered to be congeneric, at least in part, with the New World *Bagisara* Walker, 1858. This possible synonymy is complicated by the type species of both genera being somewhat atypical. Described as new are *Bagisara praecelsa*, from Texas and northeastern Mexico, and *Bagisara brouana*, from Louisiana and Mississippi. An identification key is provided for the 19 described New World species, which occur mostly in North and Central America. Taxonomic changes include two new synonymies, one new combination, one revised status, and removal of the unrelated Central American *Xanthia patula* Druce from the genus *Bagisara*.

Additional key words: moths, taxonomy, *Bagisara*, *Xanthodes*, Malvaceae.

The 17 described species of the genus *Bagisara* Walker comprise the New World component of the subfamily Bagisarinae (Crumb 1956:76, Poole 1989 vol. 1:154, Kitching & Rawlins, 1997). Nine of these are listed as occurring north of the Mexican border (Franclemont & Todd 1983:134). Two new species described in this paper enlarge the genus to 19 species and increase to 11 the number of species recorded from the United States. Two or three additional species from the neotropics are unidentified and probably undescribed.

The Bagisarinae are a peculiar group with respect both to larval morphology and adult genitalia. Forbes (1954:170) treated them as one of his "isolated genera" within a broad concept of the Acontiinae. Franclemont and Todd (1983:134) regarded them as a tribe of the Acontiinae, although Crumb (1956:4, 76) had earlier elevated the group to subfamily rank because of unusual larval features and proposed the name Bagisarinae. Poole (1989:154) followed Crumb and maintained subfamily rank for *Bagisara*, while keeping the closely related Old World genus *Xanthodes* Guenée in the subfamily Chloephorinae. Common (1990:457) also included *Xanthodes* in the subfamily Chloephorinae. Kitching and Rawlins (in press) include both *Xanthodes* and *Bagisara* in the Bagisarinae, a conclusion with which I agree.

The larva lacks prolegs on abdominal segments three and four, a condition not unusual in Noctuidae, including acontiines, and the uniordinal crochets on each of the remaining prolegs are appendiculate, each bearing a large, subapical tooth. However, some Acontiinae, including *Amyna* Guenée, also have the subapical tooth (Gardner 1946:65–68). The SV group has two setae instead of one on abdominal segment 7,

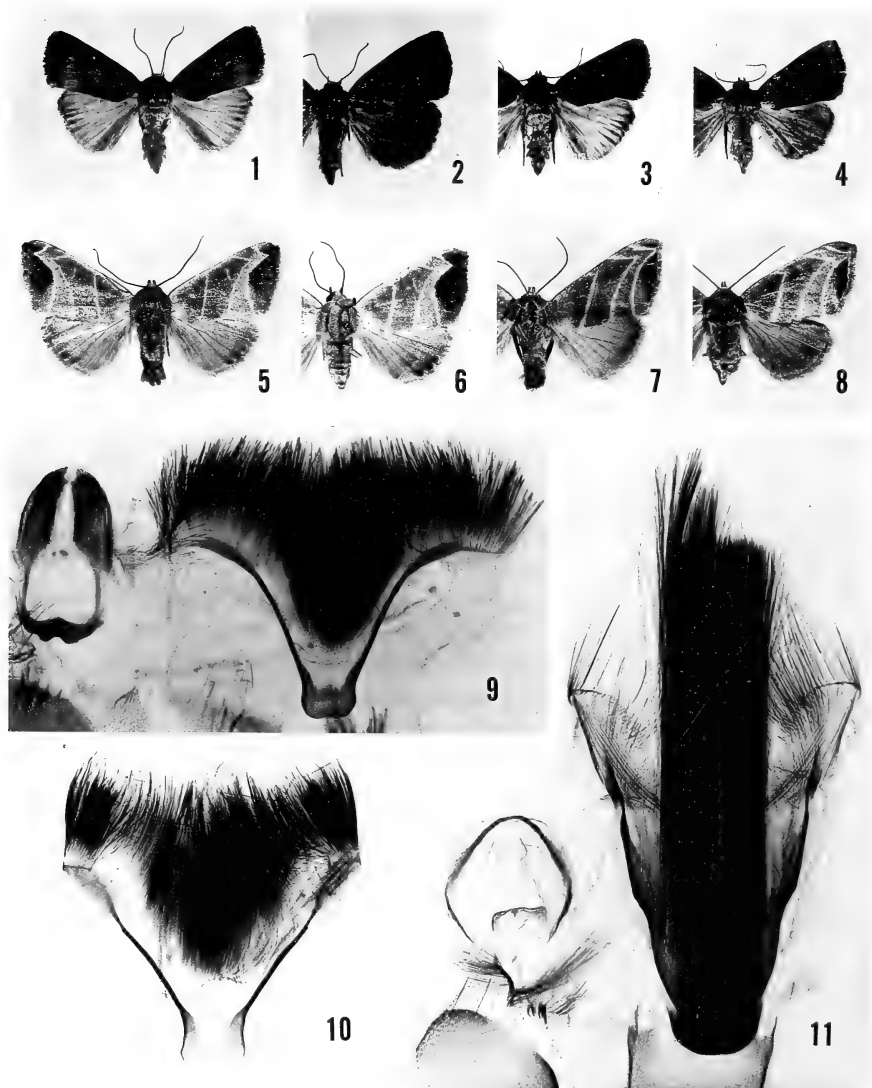
agreeing in this respect only with those of *Acronicta* Ochseneheimer, *Rivula* Guenée, and the Agaristinae among known noctuid larvae (Crumb 1956:4, 76, pl. 4A, Godfrey 1987:550). The third segment of the labial palp in the larva is unusually long, at least three times as long as the basal segment. However, these morphological observations were based on few species. Crumb (1956) appears to have had larvae of only one species, *Bagisara rectifascia* (Grt.); and can we be sure that it was not the superficially similar, more common, but atypical *B. repanda* (F.)? I found no voucher specimens.

The few recorded host plants are species of Malvaceae. The Old World species (of *Xanthodes*) also are reported to feed on Malvaceae, including cultivated cotton (*Gossypium*) and *Hibiscus*; and an Australian species, *Xanthodes congenita* (Hamp.), feeds on *Brachychiton paradoxum* Schott (Sterculiaceae) (Cacao family) (Common 1990:457).

The male genitalia (Figs. 12–17) have a distinctive configuration, with the valves usually fused together on the mesoventral (saccular) margin so that they cannot be spread apart in dissection without damage or distortion. The juxta is not recognizable. Each valve usually has 3–4 apices or preapical processes, these being the membranous apex, the rounded free distal end of an apparent costal sclerite, and one or two more slender, elongate processes that may represent the clasper or digitus. Not all processes are present in all species. Large, eversible coremata, opening laterally, reside in the bases of the valves of some species but are missing in *D. brouana* n. sp., *rectifascia*, and *repanda*. The eighth segment of the male abdomen has an elaborately modified, broom- or fan-shaped, usually heavily setose (hairy) sternite in the eighth sternum, as well as a ringlike or U-shaped eighth tergite (Figs. 9–11). The females have a conspicuous, characteristic bulla seminalis that may be delicately ornamented with encircling bands of fine, radiating, fanlike, sclerotic rods.

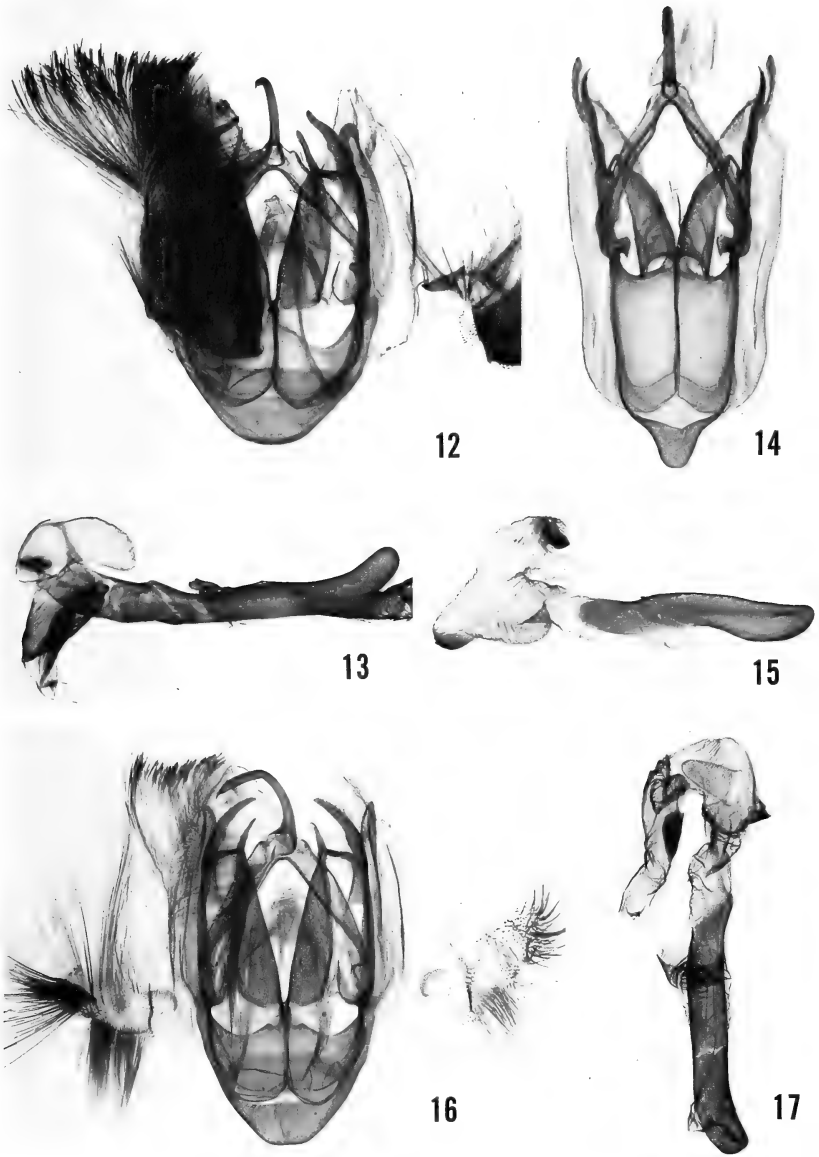
The moths have smooth, cylindrical, upturned palpi that exceed the upper margin of the front to about the level of the basal antennal segment. The antennae are simple, filiform, and minutely setose in both sexes. The legs have long, shaggy vestiture on the femora and tibiae in all species examined except *B. repanda*, in which the scaling is smooth. *Bagisara repanda* is also unusual in having a large, conspicuous patch of black-tipped scales on the front surface of the male foretibia.

While American members of this complex have continued to be treated as a single genus in the Bagisarinae or Bagisarini, their similar Old World relatives have been referred in recent years to the Chloephorinae (e.g., Poole 1989, vol. 2:991, Common 1990:457). My observations during preparation of this paper convinced me that the Bagisarinae and at least part of the species in the Old World genus *Xanthodes* belong not only to the same subfamily, but to the same genus.



FIGS. 1-8. *Bagisara* species. 1, *B. brouana*, holotype. 2, *B. brouana*, ♀ paratype, 4.2 mi. NE of Abita Springs, St. Tammany Parish, Louisiana, 7 June 1984, V. A. Brou. 3, *B. brouana*, ♂ paratype, Lizana, Harrison Co., Mississippi, 1 July 1991, R. Kergosien. 4, *B. brouana*, ♀ paratype, same data as for Fig. 3 but collected 19 July 1991. 5, *B. praecelsa*, holotype. 6, *B. praecelsa*, ♀ paratype, Mt. View Acres, San Antonio, Texas, 9 September 1971, A. & M. E. Blanchard. 7, *B. gulfare* ♂, Ames, Iowa, 4 July 1964, W. S. Craig. 8, *B. gulfare* ♀, Lacon, Illinois, 10 July 1967.

FIGS. 9-11. *Bagisara* species, ♂ abdominal structures. 9, *B. praecelsa*. 8th abdominal segment: tergite (left), sternite (right). 10, *B. gulfare*, sternite of segment A8. 11, *B. brouana*. 8th abdominal segment: tergite (left), sternite (right).



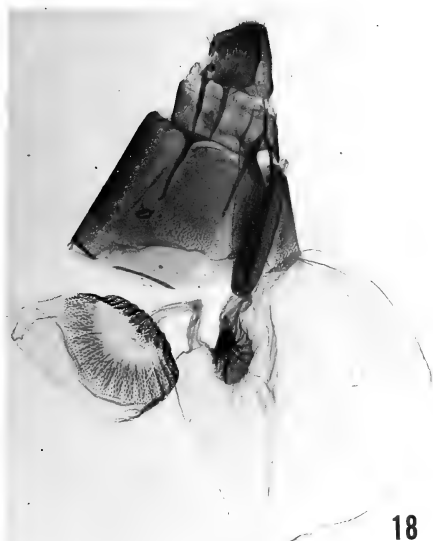
FIGS. 12-17. *Bagisara* species, ♂ genitalia. 12, *B. gulnare*. 13, aedeagus of same specimen. 14, *B. brouana*. 15, aedeagus of same specimen. 16, *B. praecelsa*. 17, aedeagus of same specimen.

Similarity of larval characters was first noted by Crumb, based on comparison of his observations with those of Gardner (1946, 1948) in India. However, the unique genitalia appear to have been neglected. *Xanthodes transversa* Guenée, a colorful, well-known tropical Asian and Indo-Australian species that ranges north to Japan, is similar to *Bagisara* species in all essential details, including the complex genitalia of both sexes. The moths have the same kind of wing pattern, and the larvae of *Xanthodes* and *Bagisara* species have related food plants: mainly species of Malvaceae.

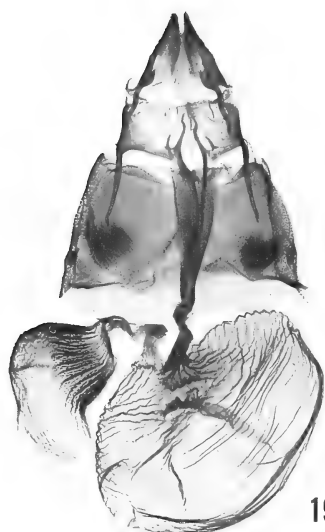
I do not synonymize *Bagisara* to *Xanthodes* in this paper because more revisionary work is needed, especially on the Old World species. Indeed, the type species of both *Bagisara* and *Xanthodes* are somewhat atypical, leaving doubts as to what the limits of the genus or genera should be. The type species of *Xanthodes* Guenée, 1852, is *Phalaena malvae* Esper [1796], now known as *Xanthodes albago* (Fabricius 1794), of the Old World tropics to the Palearctic, including southern Europe. In *X. albago* the valves are not fused together along their outer saccular margins, although closely approximate, and the distinctive sclerites (tergite and sternite) as shown in Figs. 9, 10, are not developed. The 12 Old World species of *Xanthodes*, as listed by Poole (1989), appear more diverse than their American counterparts.

The type species of *Bagisara* Walker, 1858, is *B. incidens* Walker, which is a junior synonym of *Bagisara repanda* (Fabricius 1793), a widespread and generally abundant neotropical species that reaches the southeastern USA. It differs from other American species in its smooth vestiture, somewhat different genitalia (e.g., no long processes on valve), slightly angulate outer margin on the forewing, and in having a patch of specialized black scales on the foretibia.

The following key should help in the identification of all species currently assigned to *Bagisara*. One new combination and four changes in synonymy are made in the key, and *Xanthia patula* Druce (1898:486, pl. 94, fig. 14), from southern Mexico, Guatemala, and Costa Rica, is removed from *Bagisara*, where it was placed by earlier authors. Its genitalia are very different from those of the Bagisarinae and of a more conventional type. I could not place it to genus, but am sure that the species belongs somewhere in the large assemblage long known as the Amphipyrrinae but now probably within the expanded concept of the Hadeninae of recent authors (e.g., Kitching & Rawlins, in press). It has a rich golden orange-brown forewing with darker brown markings and two white spots in the reniform. Otherwise all species and their synonymy remain as listed by Poole (1989), and the reader is referred to that work for nomenclatural detail that is not repeated here. Poole's catalogue also provides references to illustrations for about 12 of the 19



18



19



20



21

FIGS. 18–21. *Bagisara* species, ♀ genitalia. 18, *B. praecelsa*, with modified scale patches of seventh sternum removed. 19, *B. praecelsa*, with modified scale patches in place. 20, *B. gulnare*. 21, *B. brouana*.

species plus *Xanthia patula* Druce (although the figure cited for *B. demura* is misidentified, as mentioned later). To these may be added the colored illustrations of *B. gulfare* and *B. rectifascia* by Rings et al. (1992, pl. 13, figs. 20, 25). Most species are easily identified by differences in size, color, wing pattern, and other features as used in the key.

KEY TO NEARCTIC AND NEOTROPICAL SPECIES OF *BAGISARA* BASED ON SUPERFICIAL FEATURES

1. Postmedial line of forewing sharply or abruptly angled on R_5 or M_1 2
 - 1'. Postmedial line with a more rounded curve, not abruptly angled 11
 2. Forewing greenish, olivaceous, or brownish gray; transverse lines whitish or at least paler than ground color (if forewing brown, transverse lines bicolored whitish and orange); forewing with or without darkened patch having pronounced brassy sheen in subterminal area of forewing 3
 - 2'. Forewing reddish brown to gray brown, or pale with brown markings; transverse lines darker than ground color; forewing never with darkened patch with brassy sheen in subterminal area 6
 3. Forewing greenish or olivaceous; transverse lines pale, not bicolored; forewing with transversely elongate patch in subterminal area that is darker than rest of wing and has brassy sheen; hindwing grayish (an unidentified species from Paraguay, probably undescribed, would key to couplet 4 except that it lacks the darkened subterminal area with brassy sheen) 4
 - 3'. Forewing usually reddish brown with transverse lines plain or bicolored; forewing without darkened patch with brassy sheen in subterminal area; hindwing reddish brown, although paler than forewing 5
 4. Angle of subterminal line reaching outer margin, antemedial line angled before costa; dark zone with brassy sheen between subterminal line and outer margin of forewing not strongly contrasting with rest of wing. Wing length 15–18 mm. Midwestern U.S. *gulfare* (Stkr.)
 - 4'. Angle of subterminal line not reaching outer margin, antemedial line straight or only slightly bent upon approaching costa; dark zone with brassy scales between subterminal line and outer margin of forewing strongly contrasting with paler color of rest of wing (as in *B. albicosta*). Wing length 14–17 mm. Texas, Mexico *praeclata*, n. sp.
 5. Transverse lines of forewing bicolored, orange brown on proximal side, whitish or gray white on distal side. Wing length 16–19 mm. Central Mexico to Honduras *laverna* (Druce)
 - 5'. Transverse lines of forewing plain, not bicolored. (Similar to *B. laverna* or more grayish, paler hindwing). Wing length 15 mm. Cuernavaca, Morelos, Mexico *malacha* (Druce)
- (Note: Two species are figured in the literature as *B. malacha*, and I assume that the original one (Druce 1889, pl. 28, fig. 14) is correct, although I have not seen specimens. The species shown by Draudt (1926, pl. 44, row a) is *B. oula*. Druce (*ibid.*, p. 305) described the forewing as having "three narrow dark brown lines," but his figure shows the usual pale lines of this group, perhaps with only a thin, dark edging. *B. malacha* appears close to *B. laverna* but smaller, and it is without the feature of the orange-brown margin on the transverse lines, which I describe as bicolored).
6. Male forefemur with large tuft of long, reddish-brown scales, and male forewing with squarish black spot on costa between base and antemedial line (often reduced, missing, or rubbed off); forewing otherwise pale with reddish-brown markings and a characteristic double longitudinal streak through angles in post-medial and subterminal lines. Wing length 12–13 mm. Texas and Arizona to Argentina *tristicta* (Hamp.)

- 6'. Male forefemur without large scale tuft, and male forewing without black costal spot; forewing reddish brown to yellowish or gray brown, without a double or usually any streak through angle of postmedial and antemedial lines (except *graphicomas*, which has one dark streak) 7
7. Forewing dark reddish brown or dusted with brown scales against a paler background; angle of postmedial line less than 90°; forewing with dark longitudinal streak through angles of postmedial and subterminal lines; hindwing light reddish brown with thin, darker brown postmedial and subterminal lines, the former angled to mimic that of forewing (the only species with such a pattern on hindwing). Wing length 15–17 mm. Guerrero, Mexico *graphicomas* (Dyar)
- 7'. Wings reddish brown to gray brown or yellowish; angle of postmedial line acute or obtuse; forewing without dark longitudinal streak through angles of postmedial and subterminal lines; hindwing without markings. Wing length variable. Widespread 8
8. Both wings bright reddish brown, hindwings paler but almost uniformly colored; forewing with well-marked, clearly defined, regular, dark-brown, transverse lines; angle in postmedial line of forewing usually 90° or less (acute) 9
- 8'. Forewing light violaceous gray brown to yellowish brown; hindwing whitish, progressively shading to pale brownish distally; forewing with thin, delicate, regular, brown transverse lines; postmedial line acutely or obtusely angled 10
9. Wing length 18–19 mm. Orizaba, Veracruz *ochracea* (Schaus)
- 9'. Wing length 15 mm. SW U.S. to Mizantla and Guadalajara, Mexico .. *demura* Dyar (Note: *B. ochracea* and *B. demura* appear exactly alike except for size, but only females were available during preparation of key. *Bagisara ochracea* (Schaus 1906) is a **new combination**. It was described as *Trileuca ochracea* Schaus and referred to the genus *Schinia* by Poole (1989). *Bagisara xan* Dyar, 1913, is a junior synonym of *Trileuca ochracea* Schaus, and this is a **new synonymy**. These changes are based on reexamination of the types in the U.S. National Museum of Natural History. Draudt's figure (1926, pl. 44, row b) of *B. demura* is not that species but is *B. anotla*; and his figure of *anotla* (1926, pl. 44, row b) is *B. ochracea*. An unidentified species similar to *B. ochracea*, but with more oblique lines, will key out here. It has been taken in southern Minas Gerais, Brasil (USNM)).
10. Forewing light gray brown with faint violaceous tint; angle of postmedial line often less than 90°; antemedial line usually angled before costa. SW U.S., Mexico *oula* Dyar
- 10'. Forewing light yellowish brown; angle of postmedial line about 90°; antemedial line usually bent but not angled before costa. SW U.S., Mexico *buxea* (Grt.)
11. Transverse lines of forewing whitish, or at least paler than ground color 12
- 11'. Transverse lines of forewing brown to blackish, darker than ground color, sometimes not entirely distinct 16
12. Male foretibia and forefemur with large, dense, black-tipped scale tufts; outer margin of forewing slightly angulate; small, wing length 10–12 mm. SE U.S., West Indies and Mexico to Paraguay *repanda* (F.)
- 12'. Male foretibia and forefemur without large scale tufts; outer margin of forewing not angulate. Wing length variable 13
13. Antemedial line of forewing farther from base at costa than at inner margin. SW U.S. to Venezuela *albicosta* Schaus (Note: *B. albicosta* is the only species in which antemedial line of forewing is slanted in reverse direction from what is usual. Coloring of forewing closely similar to that of *B. praeclsa*, including even the dark subterminal area with brassy sheen, but course of lines is different).
- 13'. All transverse lines of forewing approximately erect from inner margin and subparallel, if visible 14
14. Wings dark brown; lines pale but faint. Small, wing length 11 mm. Guyana, Costa Rica *obscura* Hamp. (Note: *B. obscura* has the appearance of a very dark-suffused *B. repanda*, but the outer margin of the forewing is evenly rounded, not angulate. The wing shape and pattern, although indistinct, appear much as in *B. rectifascia*).

- 14'. Wings light brown with distinct, pale (or partly pale, partly darker) transverse lines. Wing length 12–14 mm 15
15. Forewing with inner margin straight or slightly convex; outer margins evenly rounded, tornus rounded; hindwing normal, not appearing produced or unusually triangular. U.S. to Nicaragua and Costa Rica (may not all be same species) *rectifascia* (Grt.)
- 15'. Forewing with slightly concave inner margin and relatively sharply angled tornus; outer margins of both wings not entirely rounded but with places where they are straight or very slightly concave; hindwing appearing more triangular, with anal angle about 90° and not or hardly rounded. SW U.S. to Costa Rica . . . *pacifica* Schaus
16. General wing coloring very dark, blackish, lines present but obscure. Wing length 13–15 mm. Louisiana, Mississippi *brouana*, n. sp.
- 16'. Much paler, pale brown to reddish brown. Wing length 13–17 mm. Neotropical 17
17. Very pale brown with thin, regular, erect, subparallel darker brown lines on forewing. Wing length 12–15 mm. Panama, Brasil, Venezuela . . . *paulensis* (Schaus)
- 17'. Light reddish-brown moths with smudgy markings and lines often indistinct. Guatemala to Panama 18
18. Deep reddish-brown suffusion across much of forewing except costal area, and patch of blackish to dark-gray scales in median space near inner margin; hindwing whitish toward base, shading to yellowish brown distally. Small, wing length 13–15 mm. Guatemala, Panama *avangareza* Schaus
- 18'. Forewing without dark shades except some deep reddish brown near outer margin; hindwing bright orange brown, not or hardly paler toward base. Larger, wing length 16–17 mm. Mexico, Guatemala, Panama *anotla* Dyar
(Note: *Bagisara lulua* Schaus, 1921 is a junior synonym of *B. anotla* Dyar, 1914, **new synonymy**, and the latter is a separate species, **revised status**, not a synonym of *B. demura* Dyar, 1913, as indicated by Poole (1989:154). This is based on a reexamination of the Schaus and Dyar types in the U. S. National Museum, but few specimens are available and most are females. The figure of *B. lulua* by Draudt (1926, pl. 44, row b) is a good likeness of *B. anotla*).

***Bagisara praeclsa* Ferguson, new species**

(Figs. 5, 6, 9, 16, 17, 18, 19)

Diagnosis. This species resembles *Bagisara gulfare* (Strecker) and was misidentified as that species in collections. However, the two apparently are not sympatric, as the true *B. gulfare* is known from Ohio, Michigan, Illinois and Iowa, whereas *B. praeclsa* occurs in Texas and northern Mexico. They are easily distinguished by differences in the forewing pattern. The antemedial line is straight or only slightly incurved near the costa in *praeclsa*, sharply angled near the costa in *gulfare*. Also, in *praeclsa*, the angles in the postmedial and subterminal lines are offset relative to each other; the outermost point of the postmedial is no farther out than the point at which the subterminal meets the costa, and the outermost point of the subterminal usually stops short of the outer margin. In *gulfare*, the angulate part of the postmedial fits within that of the subterminal with almost perfect symmetry, the point of the postmedial surpasses the point where the subterminal meets the costa, and the outermost point of the subterminal reaches the outer margin. In *praeclsa*, the contrasting zone of metallic scales between the submarginal band and the outer margin is larger as a result of the submarginal band being more deeply incurved, and it is deep metallic red brown rather than gold colored. Although males of both species differ from all other U.S. *Bagisara* in having a distinct patch of erect scales on the hindwing between the second and third anal veins about a third of the way out from the base, these scales are yellow in *praeclsa* and light grayish brown in *gulfare*. The complicated genitalia of *praeclsa* are similar to those of *gulfare* in both sexes, but differ in the shape and proportions of many parts.

Further description. Antenna simple in both sexes; male palp brushlike, tufted with stiff, hairlike scales on ventromesial surface; alula-like structure (posterior to base of hindwing on each side) bearing an expandable tuft of long, yellow-brown scales matching in

color the erect scales on hindwing and transverse dorsal intersegmental bands on abdominal segments 5–8; tegula short compared to that of at least some other species of *Bagisara*, not reaching base of abdomen; all foregoing features common to *gulfare* and *praeceles*, except that sex scales in *praeceles* are bright-yellow instead of gray-brown. Forewing light, lustrous, olivaceous gray, finely dusted with white scales, traversed by three thin, clearly defined transverse lines, and with a submarginal, lunate, metallic, dark coppery-brown patch about as wide as minimal distance between antemedial and postmedial lines (narrower in *gulfare*). Other forewing markings as described in diagnosis. Hindwing gray brown, often slightly darker toward outer margin, and with a terminal series of vague whitish dots or wedges between vein endings (rather than the continuous, slightly sinuous, whitish terminal band apparent in fresh specimens of *gulfare*). Length of forewing: holotype, 16 mm; other ♂♂, 14–17 mm ($n = 25$); ♀♀, 16–17 mm ($n = 7$).

Male genitalia (Figs. 9, 16, 17). Differing from those of *Bagisara gulfare* (Figs. 10, 12, 13) most obviously as follows: overall shape of valve and its everted corema more slender, and corema with hair tufts only half the size of those in *gulfare* (cut off in Fig. 12); valve with rounded end of costal lobe produced beyond end of most mesial of the slender, bladelike, preapical, valvular processes; vesica with two sclerites of nearly equal size (unequal in *gulfare*), and a diverticulum smaller than that of *gulfare*. Sclerites of eighth tergum and sternum also differ, as illustrated.

Female genitalia (Figs. 18, 19). Similar to those of *Bagisara gulfare* (Fig. 20) in most respects, but easily distinguished by the smaller, less persistent, paired scale tufts on sternum 7. These tufts are large, dark colored, and difficult to remove in *gulfare* (Fig. 20); smaller, paler, and more nearly deciduous in *praeceles*. Also, in *praeceles*, posterior margin of sternum 7 relatively shallowly emarginate at ostium; outer two of four needlelike sclerites arising from ostium being one-third to four-fifths as long as middle pair; corpus bursae at juncture with ductus bursae bearing a relatively prominent sclerite marked with a fanlike, radiating pattern of ridges.

Types. Holotype ♂, Fort Davis, Jeff Davis Co., Texas, 11 July 1969, A. and M. E. Blanchard. Paratypes: 6 ♂♂, same locality and collectors, 30 July 1964, 25 June 1965, 11 June 1969, 28 August 1970; 1 ♀, same locality, 19 August 1984, E. C. Knudson; 2 ♂♂, Mount Locke, 6700', Davis Mountains, Texas, 10 June 1969, A. and M. E. Blanchard; 4 ♂♂, 1 ♀, Alpine, Brewster Co., Texas, 10 June 1969, 2 August 1964, 6 Sept. 1964, 10 September 1963, same collectors; 1 ♂, Bear Canyon, Guadalupe Mountains, Texas, 4 September 1969, same collectors; 2 ♂♂, McKittrick Canyon, Guadalupe Mountains, Texas, 29 August 1967, same collectors; 1 ♀, Sierra Diablo Wildlife Management Area, 6000', Culberson Co., Texas, 5 June 1969, same collectors; 2 ♂♂, Junction, Kimble Co., Texas, 24 August 1973, same collectors; 3 ♂♂, 1 ♀, Mt. View Acres, San Antonio, Texas, 30 August 1973, 9 Sept. 1971, same collectors; 1 ♀, Kerrville, Texas, June 1919; 1 ♂, San Benito, Texas, 16–23 March [incorrect date?]; 1 ♂, Bentsen-Rio Grande Valley State Park, Hidalgo Co., Texas, 27 May 1982, E. C. Knudson; 6 ♂♂, 2 ♀♀, Limpia Canyon, Davis Mountains, Jeff Davis County, Texas, 4920', 30° 17.4' N, 103° 36.6' W, 9 August 1991, E. H. Metzler; 1 ♀, 3 mi. E Galeana, 5000', Nuevo Leon, Mexico, 7–9 August 1963, [W. D.] Duckworth and [D. R.] Davis. Holotype and most paratypes in collection of U. S. National Museum of Natural History; some paratypes returned to E. C. Knudson, E. H. Metzler, and deposited in other museum collections; namely, the Canadian National Collection, Ottawa; American Museum of Natural History, New York; Carnegie Museum, Pittsburgh; Cornell University, Ithaca, New York, and The Natural History Museum, London.

Distribution. This species has a wide distribution within Texas, as the above listed localities indicate. Otherwise, I have seen it only from Mexico, where the one paratype was collected about 95 km south of Monterrey and 240 km from the U.S. border.

Early stages. Undescribed. The larva of *B. gulfare* feeds on foliage of glade mallow, *Napaea dioica* L. (Malvaceae). One specimen was reared from a larva found on this plant in remnant wet prairie in Pickaway County, Ohio by E. Metzler, and the moth is regarded as an endangered species in Ohio (Rings et al. 1992:71). The larva is green with a vague, yellowish lateral stripe.

Remarks. *Bagisara laverna* (Druce), of Mexico and Central America, is the species most similar to *B. gulfare* and *B. praeceles* in size, color, and pattern. *Bagisara albicosta*

Schaus, although nearly identical to *B. praecelsa* in size and especially coloring, has different transverse lines (see key). If the apparent allopatry of *praecelsa* and *gulfare* proves to be real, then these two species may be distinguished by locality label. I examined specimens of *B. gulfare* from four states, as follows: OHIO: 30 mi. S of Columbus (emerged 12 Aug. 1989, 1 specimen in Metzler coll.). MICHIGAN: Berrien County (26 June–14 July, 3 specimens, J. H. Newman, in Metzler coll.). ILLINOIS: Champaign; Elgin; Lacon; Peoria; Putnam Co.; Quincy; Urbana (9 June–1 Sept., 73 specimens in Illinois Natural History Survey collection and U. S. National Museum of Natural History). IOWA: Ames; Milford; Soldier (4 June–2 Sept., 8 specimens in U.S. National Museum of Natural History). *Bagisara gulfare* has also been recorded from Pennsylvania (Tietz [1952]:83; Forbes 1954:264), but this needs verification. Neither *gulfare* nor *praecelsa* appears to have been identified or recorded in the literature from any of the intervening states such as Missouri, Mississippi, Arkansas, Kansas, and Oklahoma, although doubtless there are records that I have not seen.

***Bagisara brouana* Ferguson, new species**

(Figs. 1–4, 11, 14, 15, 21)

Diagnosis. A large, distinctive, dark-brown species known only from St. Tammany and Tangipahoa Parishes, Louisiana, where many have been collected over a period of years by the collector for whom it is named, and from Hancock and Harrison counties, Mississippi, where it was collected by R. Kergosien. The forewing pattern of three narrow, subparallel, transverse bands is generally similar to those of *B. rectifascia* and *B. repanda*, but the bands are largely blackish on a dark-brown background, not pale on a light-brown background as in those species. The bands are often inconspicuous because of the overall dark suffusion. *Bagisara brouana* is unique in being sexually dichromatic with respect to wing color, the males being distinctly lighter on both fore- and hindwings. In our fauna it is most closely related to *B. rectifascia*, and, like that species, has unmodified vestiture on the male foreleg and an evenly convex outer margin on the forewing. *Bagisara repanda* differs in having a conspicuous patch of long black scales on the male front femur and a somewhat angulate outer margin on the forewing.

Further description. Male foreleg unmodified, without unusually long or specialized scales, and without a femoral tuft of black scales. Antennae and other external structures as in related species. Forewing of both sexes with outer margin evenly convex, not angulate near middle as in *B. repanda*, dark reddish brown (blackish) with a violet iridescence in fresh specimens; discal spot transversely oblong, blackish, diffuse; the three transverse bands narrow, blackish (sometimes partly shadowed by a pale shade), almost erect relative to inner margin, and in nearly the same positions as the pale bands of *B. rectifascia*; antemedial band straight or slightly concave, about one-third of the way out from base; postmedial band just beyond discal spot, slightly concave except toward costa, where it curves basad; subterminal band meeting inner margin at or near tornal angle in *B. brouana* and *B. rectifascia* (midway between postmedial band and tornal angle in *B. repanda*); an incomplete terminal row of small black dots usually present; males often with space between postmedial and subterminal bands occupied by a slightly paler, violaceous-brown shade that may form an almost complete pale band (as in holotype) or be confined to a patch near inner margin; fringe concolorous with wing or darker. Hindwing sexually dimorphic in shape and coloring; that of male with outer margin often nearly straight between M_1 and first anal fold; light yellowish brown, glossy, with dusky shading near inner margin and, in most fresh males, with gray, elongate, wedge-shaped rays toward outer margin and between veins; female hindwing with outer margin evenly and roundly convex, and the color uniformly dusky brown, nearly as dark as forewing; discal spot wanting in male, nearly so in female; fringes concolorous. Scales of thorax concolorous with forewing, of abdomen concolorous with hindwing. Underside pale, dusted with darker gray-brown scales, with discal spots developed on both wings, and with rounded, evenly convex, parallel, dark-brown postmedial bands variably developed on both wings, poorly so in males, often half-developed on forewing and fully developed on hindwing in females. Length of forewing: holotype, 13.5 mm; other ♂♂, 13–15 mm ($n = 18$); ♀♀, 12–15 mm ($n = 57$).

Male genitalia (Figs. 14, 15). Similar to those of other species of *Bagisara* examined inasmuch as the ventral margins of the valves are fused together so that the valves cannot be spread apart without damage and distortion. Genitalia most closely resemble those of *B. rectifascia*, but are greatly elongated to 1.5 times length from saccus to uncus, with all components proportionately elongated, including aedeagus. The complex eighth sternite (Fig. 11) similar in form but also elongated, its posterolateral apices not flared outwardly as much or as abruptly as those of *B. rectifascia*. Male genitalia differ in shape of virtually all parts from those of *B. repanda* and *B. buxea*. Eighth sternite and tergite are both complex in this genus, but in *B. brouana* and *B. rectifascia* are especially conspicuous; eighth sternum of these species bears a partly sclerotized structure (sternite) forming an elongated, funnel-shaped structure with a large, medial, posteriorly directed tuft, probably the corema associated with a scent gland; eighth sternite of *B. repanda* with a similarly situated but smaller tuft, comprised mainly of long, spatulate scales. *Bagisara brouana*, *rectifascia*, and *repanda* all lack the coremata arising from the bases of the valves in *B. buxea*, which clearly is not a closely related species.

Female genitalia (Fig. 21). As illustrated.

Types. Holotype ♂, 4.2 mi. NE of Abita Springs, Sec. 24, T6 SR12E, St. Tammany Parish, Louisiana, 8 August 1983, V. A. Brou. Paratypes: 17 ♂♂, same locality and collector, 4, 11, May, 6, 11, 18, 19, 23 June, 2, 7, 27 July, 8, 9, 11, 13 August, 2 September 1983; 17 ♂♂, same locality and collector, 5, 7, 14, 22, 29, 30 May, 7, 9, 10, 14, 21, 18 June, 21, 22 July, 8, 30 August, 1 September 1984; 10 ♀♀, same locality and collector, 22 May, 6, 9, June, 1, 16, 26 July, 1, 8, 14, 20 August 1984; 15 ♀♀, same locality and collector, 26, 29 April, 13, 22, 28 May, 3, 6, 7, 20, 22 June, 18, 19 July, 1 August 1984; 2 ♀♀, Fluker, Tangipahoa Parish, Louisiana, 12 May 1978, V. A. Brou; 30 ♂♂, 10 ♀♀, Lizana, Harrison County, Mississippi, 16 June–17 August 1991, R. Kergosien; 6 ♂♂, 7 ♀♀, Long Beach, Harrison County, Mississippi, 30 June–20 August 1991, R. Kergosien; 1 ♂, Blk. Crk. near George-Jac[kson] Co. line, Jackson County, Mississippi, 1 August 1991, R. Kergosien; 1 ♀, Pass Christian, Harrison County, Mississippi, 19 July 1979, R. Kergosien; 1 ♀, Bay St. Louis, Hancock County, Mississippi, 16 July 1979, R. Kergosien. The Louisiana specimens were all collected in light traps using mercury vapor lamps and ultraviolet fluorescent tubes. Holotype and some paratypes in collection of U.S. National Museum of Natural History; remaining paratypes mostly in collection of V. A. Brou, Bryant Mather, and R. Kergosien, but some will be distributed to other collections as mentioned under *B. praeclsa*. Fifteen additional specimens from the type locality were examined but not labelled as paratypes because of their poor condition.

Distribution. Known only from the Louisiana and Mississippi localities listed above.

Early stages. Unknown. *Bagisara rectifascia* has a slender green semilooper larva, with the first two pairs of prolegs missing, reported on *Hibiscus lasiocarpus* Cav. and *Malvaviscus drummondii* T. & G. (both Malvaceae) in Texas (Crumb 1956:77). Larva of *B. buxea* reported on a species of *Sphaeralcea*, also in the Malvaceae (Comstock & Dammers 1935:138).

Remarks. A curious feature of this species is its restricted distribution. Intensive collecting in the southern States in recent years has failed to reveal its presence anywhere outside of the three coastal counties of Mississippi and two nearby parishes of Louisiana, as far as I am aware. However, nearly 200 specimens collected by Brou in two seasons at the type locality indicate a large and thriving local population. It may be a specialized feeder on one genus or even one species of plant that also has a limited distribution. The closely related *B. rectifascia* has a wide distribution in the eastern U.S. but is not common in collections. *Bagisara repanda* is sometimes abundant in the Southeast, particularly in Florida, and throughout the Caribbean Region and much of the American tropics. The only other species of *Bagisara* regularly present in the U.S. east of Texas and the Great Plains is *gulfare* (Strecker) (Figs. 7, 8), a similarly large but conspicuously different species with an olive-green forewing having a brassy sheen and oblique, silvery-white bands. It was further discussed above under *B. praeclsa*. *Bagisara buxea* has been reported as far north as Wisconsin (type of *delicia* (Dyar), a junior synonym of *buxea*), perhaps as a vagrant from the South or with a false locality label. *Bagisara gulfare* and *B. rectifascia* were illustrated in color by Rings et al. (1992, pl. 13, figs. 20, 25), and *Bagisara repanda* (as

Atethmia subusta Hbn.) and *B. rectifascia* were illustrated (although not very well) by Holland (1903, pl. 27, figs. 4, 5).

A summary of Louisiana *Bagisara* records to the end of 1995 sent by V. A. Brou shows an almost continuous flight period for *B. brouana* from about 6 April to 19 September, with major peaks in early and late June, lesser peaks in late May, late July, and early to mid August, and an abrupt decline in September. This would seem to reveal three or more extended, overlapping generations. Comparable data for *Bagisara rectifascia*, but with far fewer records, show a similar pattern. In contrast, the many records for *B. repanda* are mostly clustered late in the season, from late August into November, with the greatest number in September. This is the classic pattern of a seasonal immigrant from the tropics that may not overwinter in the United States.

ACKNOWLEDGMENTS

It is a pleasure to name *Bagisara brouana* after its original discoverer, Vernon A. Brou of Abita Springs, Louisiana, who brought the species to my attention and who provided all the known specimens except those subsequently sent from Mississippi by Bryant Mather. I thank E. C. Knudson (Bellaire, Texas), B. Mather (Jackson, Mississippi), and G. L. Godfrey (formerly of the Illinois Natural History Survey, Urbana, Illinois) for the loan of material; E. H. Metzler (Columbus, Ohio) for host and distribution data; and R. W. Poole (Rockville, Maryland) for comments and advice on noctuids. *Bagisara praeceles* is described mostly from material collected by the late André Blanchard and donated to the U.S. National Collection. I thank R. W. Hodges and J. Pakaluk of the Systematic Entomology Laboratory; J. G. Franclemont, Ithaca, New York; E. H. Metzler, Columbus, Ohio; J. S. Miller, American Museum of Natural History, New York; and D. F. Schweitzer of Port Norris, New Jersey for reviewing the paper. I prepared all illustrations.

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GENERAL NOTES

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EUREMA DINA LEUCE (PIERIDAE) FEEDS ON A LACTIFEROUS HOSTPLANT IN EASTERN BRAZIL

Additional keywords: feeding behavior, Leguminosae, *Mimosa*, oviposition preference.

The pantropical genus *Eurema* (Pieridae) includes 37 neotropical species (DeVries 1987) whose larvae feed primarily on plants in the Fabaceae, Caesalpinaceae, and Mimosaceae (Clark & Dickson 1965, DeVries 1985, 1987, Jones & Rienks 1987, Jones et al. 1987). In contrast to most species in the genus, the larvae of *Eurema dina westwoodi* Boisdual utilize two species of *Picramnia* (Simaroubaceae) in Costa Rica (DeVries 1985, 1987), and those of *E. hecabe phoebus* Butler are reported to feed on Euphorbiaceae in Australia (Jones et al. 1987). Brown (1992) also noted that larvae of *E. elathea* Cramer occasionally feed on Apocynaceae, but stressed that this species prefers legumes.

We studied *E. dina leuce* Boisdual in an open area and along a forest edge at the Linhares Forest Reserve (19°8'S, 40°3'W), Espírito Santo, Brazil in July 1995. We observed two females ovipositing on leaves of *Mimosa laticifera* Rizzini and Mattos (Mimosaceae), a species with lactiferous leaves, a rare trait within the Leguminosae. The 2–4 pairs of large (2–3 cm diam.) leaflets of this plant present secondary venation confluent with the marginal nerve and exude droplets of latex when leaf ducts are damaged. *Mimosa laticifera* is distributed throughout eastern Brazil southward from 7°S (Barneby 1985) and occurs as a shrub (0.1–1.0 m tall) at the study site. As far as we know, this is the first documented use of a latescent plant for a New World *Eurema*.

To test whether *E. dina leuce* showed habitat preference for oviposition, we sampled eggs and larvae on 150 plants of *M. laticifera* in an open area and on 60 additional plants along a neighboring forest edge. Oviposition site preference was evaluated using the proportion of plants with early stages of *E. dina leuce* in each area. To estimate host-plant density, we established 17 plots of 64 m² in each area and counted the number of *M. laticifera* in 5 quadrats of 0.25 m² placed systematically in each plot (one at the center and four at the corners).

We found a total of 39 eggs on the leaves of 23 of the 210 *M. laticifera* plants examined. We also encountered two first instar and two fourth instar larvae on these and two additional plants which lacked eggs. Plants with eggs averaged 17.9 cm tall (SD = 7.1, n = 23) and did not include plants in the larger size categories. Field collected eggs were white and spindle-shaped and eclosed 3.4 days (SD = 0.9, n = 14) after oviposition (data for eggs with known time of oviposition). Sixty percent of the eggs (n = 39) were on new leaves and 40% on mature leaves. Most were found singly on plants (72%) usually on the underside of leaves (87%). Eggs censused in the field showed high mortality rates: 51% of the 39 eggs disappeared before hatching and an additional 13% turned black without hatching, apparently due to parasitism.

Eurema dina leuce strongly preferred plants growing along the forest edge. As stressed by Stanton (1982), selectivity is manifested when certain resource types are utilized more often than their relative abundance would dictate. Although the density of *M. laticifera* was greater in the open area (3.8 individuals/m², SD = 1.4, n = 85) than at the forest edge (0.3 individuals/m², SD = 1.2, n = 85), only 2 of the 150 plants sampled in the open area had early stages whereas 23 of the 60 plants sampled along the forest edge harbored eggs and/or larvae ($\chi^2 = 56.4$, df = 1, P = 0.001).

Although little is known about the mechanisms of oviposition site selection in pierid butterflies, it is envisaged that females first locate appropriate habitats in which to search for host plants (Courtney 1986). Also, Pieridae frequently deposit eggs contagiously and may prefer plants growing at low densities (Root & Kareiva 1984, Courtney 1986). It seems that *E. dina leuce* females use the forest edge or some associated factor as a cue for finding host plants. The adaptative significance of this preference, if any, is unknown.

Early instar larvae of *E. dina leuce* apparently avoid latex ducts by feeding between leaf veins of *M. laticifera*. Fourth and fifth instars observed in the field chewed a notch in the rachis and waited for the latex to drip from the wound prior to feeding on a leaf. Dussourd

(1993) suggested that caterpillars that feed on lactiferous plants sever veins and cut trenches specifically to deactivate the defensive function of pressurized latex.

Although *E. hecabe phoebus*, *E. elathea*, and *E. dina westwoodi* use plants from families that characteristically produce latex (Jones et al. 1987, Brown 1992), the behavior of avoiding latex apparently has not been reported for *Eurema*. Moreover, Dussourd (1993), in a recent revision of caterpillar behavior for circumventing plant defenses, did not report any such case for pierids. This record for *E. dina leuce* suggests that complex behavior specifically directed to circumvent latex defense may evolve relatively easily even in taxa apparently unassociated with lactiferous plants during much of their evolutionary histories.

It is important to note that other legumes occurring in the study area [*Chamaecrista patellaria* Greene (Mimosaceae) and *Stylosanthes viscosa* SW (Fabaceae)] are used as host plants by *E. nise tenella* Boisdual and *E. elathea*. Also *E. albula* Cramer feeds on four species of *Senna* sp. (Caesalpinaceae) at the same locality. Why *E. dina leuce* prefers to use a host plant that produces latex deserves further investigation.

We conducted this study during the field course "Ecologia de Campo I" of the State University of Campinas (UNICAMP). K. S. Brown, Jr. identified the butterfly species, F. A. M. Santos made suggestions during the field work, and P. S. Oliveira, A. Shapiro and an anonymous reviewer provided helpful comments on the manuscript. Fellowship support to I. Andrade was provided by the Fundação de Amparo à Pesquisa do Estado de São Paulo (grant number 95/2107-7). W. Benson was supported by a research fellowship from the CNPq. We thank the Companhia Vale do Rio Doce for essential logistic support and permission to work in the Linhares Forest Reserve.

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